CHAPTER 2

DIAGNOSIS OF THE TEMPERAMENT OF TROPICAL RAIN FOREST TREES

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INTRODUCTION

In both silviculture and forest ecology, the behaviour of trees has always been considered of the utmost importance, because forests are defined by their trees. A traditional notion in European silviculture therefore is the "temperament" of a tree species. This term is used in such a self-evident way (e.g. Cochet 1959, Lanier 1986) that it is not strictly defined in the literature. From the way it is employed, the temperament of a tree may be defined as the set of growth-and-development reactions shown by a tree towards its environment during its life cycle. For each tree species, or even provenance, this requires a closer definition both of the reactions and of the environmental factors to which the tree reacts. Light is the one most used, and wood increment has been the main growth criterion. Classical examples of specific tree temperaments then are "light-demanding" versus "shade-tolerant" trees, "pioneers" versus "climax species", or tree species growing well on poor versus rich soils.

The temperament is usually pinpointed for a tree species by combining its environmental preferences, for germination and for the mature tree. For instance *Cecropia* species (Moraceae) are generally known as light-demanding pioneers, because they require open conditions with much light both for germination and in their mature phase. In classical silviculture geared to wood production, forest stands are thought to develop from a "seedling phase", through a "sapling phase" and a "pole phase" into a "mature phase", when trees can be harvested. Even in this simplified context, the neglect of the sapling and pole phase constitutes a clear gap in the understanding of tree temperaments.

In natural regeneration silviculture in tropical rain forests (e.g. de Graaf

1986, Jonkers 1987, Queensland Department of Forestry 1983), with its much more complicated forest development patterns, this gap is extremely troublesome. The environment of growing trees in rain forests often changes rapidly and profoundly during their life cycle.

SYSTEMS ANALYSIS

The subject of tropical rain forest tree temperaments cannot be dealt with in simple terms of " a tree" and "its environment". The reaction of a tree may be total and involve the whole organism or be partial and take place in a complex of organs, like a leaf-bearing branch, or at the level of the organs themselves. On the other hand, the environment of the tree does not only consist of abiotic patterns, determined by climatic and soil factors. These factors are filtered by the surrounding vegetation, composed of a patchwork of young, building, mature and decaying forest patches (e.g. see Whitmore, this volume). And within a particular patch, the incoming nutrients and energy are filtered again by many interacting organisms before they reach the tree under consideration.

This situation can be ordered systematically in terms of systems analysis. The main concept of this type of analysis, which implicitly underlies most scientific research, is that a system may be explained in terms of interactions among its subsystems. For instance, the interactions among leaf- and flower-bearing shoots or axes explain the tree crown (cf. Hallé *et al.* 1978). The hierarchy of systems and subsystems which are in turn explained by their own subsystems, cannot be treated extensively in this contribution, and the reader is referred for a more complete discussion of concepts and definitions to Oldeman (1974*a*, 1974*b*, 1979, 1983, 1990 in press) and to Hallé *et al.* (1978).

The immediate environment of a tree can be referred to as an eco-unit. This is one patch in the forest patchwork, or mosaic of patches, mentioned above. A forest eco-unit (regeneration unit) can be defined (Oldeman 1990, in press) as "every surface on which, at one moment in time, a vegetation development has begun, of which the architecture, ecophysiological functioning and species composition are ordained by one set of trees until the end" (Fig. 2.1).

This definition not only includes "patches", "gaps" or "chablis" of modest sizes, e.g., between 0.01 and 0.1 ha (cf. Shugart 1984), but extends to all deforested surfaces where forest starts to develop, e.g. also clear-cuts, cleared and abandoned lands, or intermediate-sized patches (cf. Budowski 1965). The development of patches is thought to occur in a step-wise fashion (e.g. see Whitmore, this volume), as has long been recognized in silviculture (cf. K. Gayer, ca 1888, ex Van Schermbeek 1898). The

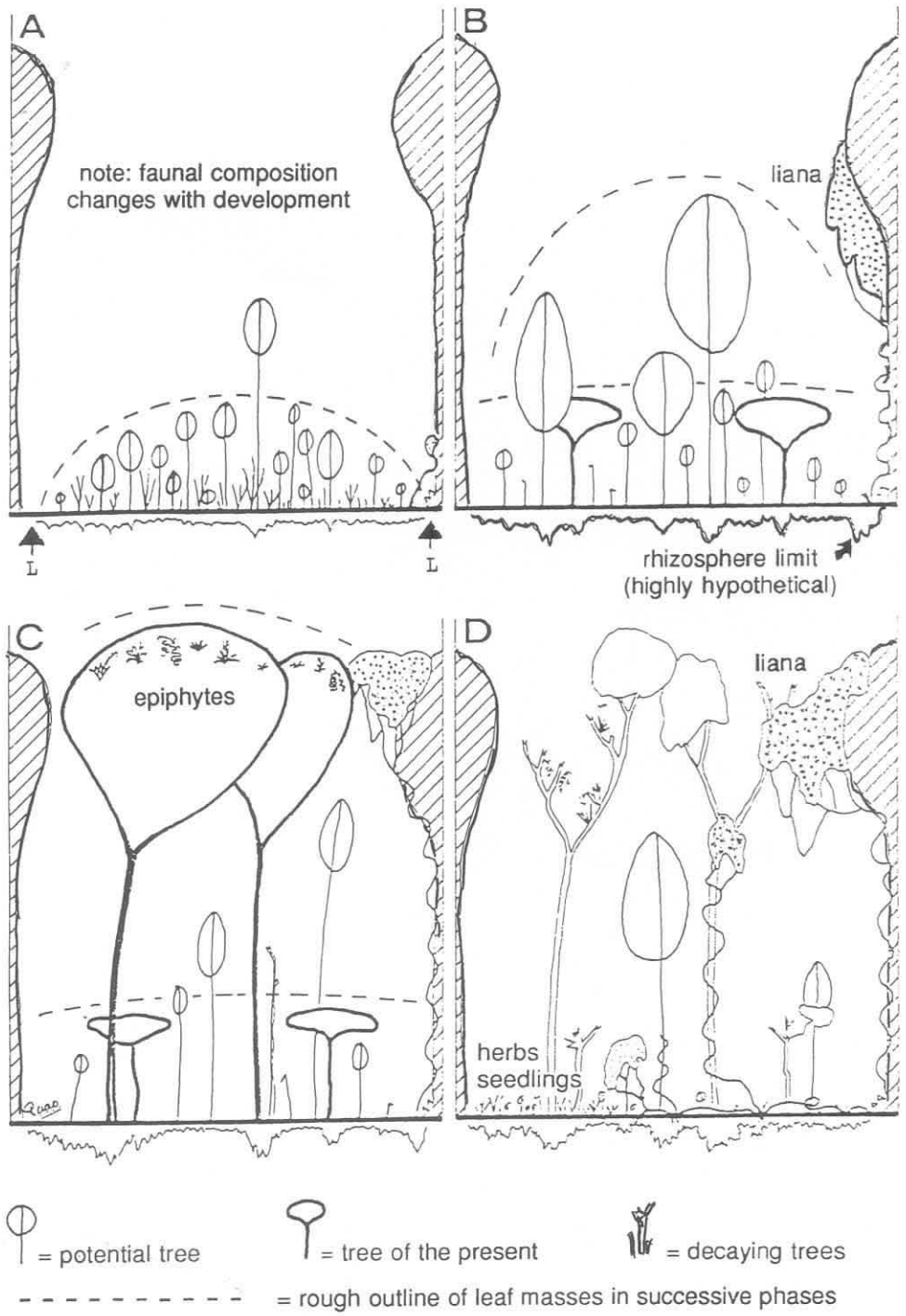


Fig. 2.1 Simplified analysis of eco-unit development, the eco-unit being the smallest coherent forest ecosystem determining the immediate environment of trees during their whole life cycle, from sapling (potential tree) to decay. Simplifications of this diagram: linear limits (L) instead of a transition zone; unrealistic unchanging surrounding forest (hatched), unrealistic low number of component organisms. A – Innovation phase ("gap phase", Whitmore, this volume); B – Aggradation phase ("building phase", Whitmore, this volume); C – Biostatic phase ("mature phase", Whitmore, this volume); D – Degradation phase (no Whitmore equivalent). Note that trees of the present, incapable of further crown expansion but stable survivors, determine layering in the biostatic phase, the younger phases not being completely layered as yet, the degradation phase no longer being layered. Eco-units occur with widely differing sizes ("gap size" at origin; cf. Fig. 2.9) and with widely varying architectures, offering many different and changing niches for growth of trees with different temperaments. From Oldeman (1990, in press)

insertion of architectural criteria in the definition is to account for different shapes of an eco-unit, e.g. funnel-shaped, cylindrical or bowl-shaped, and the differences in forest development induced by this shape. Architectural analysis begins by the mapping of the outer geometrical limits of an eco-unit and then the mapping of the geometrical disposition of internal compartments with a certain function. This allows the introduction of ecophysiological production (see Ramakrishnan, this volume) by each compartment, e.g. dominant trees (trees of the present), suppressed (potential) trees, seedlings or insects. The mode of production is determined in turn by adapted organisms which implement it, i.e. the species building an eco-unit in interaction with each other.

Although such a discrete model is only one way of interpreting forest ecosystems – continuous modelling based on gradients rather than mappable limits being another (cf. Kessell 1979, Bongers and Popma 1988) – the eco-unit approach has been chosen because it permits refinement of tree biotope analysis without rejection of the notion of gradients. Indeed, if borders between eco-units are considered to be transition zones with steep climatic, biotic and soil gradients, both approaches can ultimately be harmonized.

In the following paragraphs, eco-units are mainly categorized as small, medium-sized or large, and according to their development phase, i.e. successively as young or open, dynamic or building, mature (biostatic), and degrading. All references to quantities and qualities of incoming light or nutrients have to be seen in this context, as well as matters concerning biological competition between trees. The eco-unit is considered as the system, in a certain state, and the trees are seen as the sub-systems determining its overall function.

TREES, THEIR SUBSYSTEMS AND DIAGNOSIS OF THEIR TEMPERAMENT

The function of a tree in its forest eco-unit has to be considered in two ways. On the one hand, the tree participates in building the eco-unit and so contributes to the survival of the eco-unit. On the other hand, the tree reacts to all biotic and abiotic inputs coming from its immediate biotope. Can this behaviour be seen directly, and can a diagnosis of a tree's temperament be based upon visible and measurable symptoms?

Here again, no simple answer is possible. Trees are too complex. Different behaviour can become apparent at the level of the whole organism, of parts of the crown, of branches with their lateral organs, and of these organs. These levels are not independent of each other. As a frame of reference, their interdependence can be sketched as follows:

Organs, in interaction, build shoots. The nature of the organs, particularly leaves (photosynthesis) and flowers and fruits (reproductive strategy), is a determinant of tree temperament. But their arrangement on the shoot also has to be considered;

Shoots, in interaction, build trunks-cum-crowns. This occurs according to a limited number of constructional modes, the architectural models of Hallé and Oldeman (1970; also see Hallé *et al.* 1978). Diagnostic criteria here can be found both in shoot and crown architecture;

Crowns, in interaction, build the canopies of large trees. The process of building extra crowns in the same tree, each according to the architectural model of the tree, has been called reiteration by Oldeman (1974*a*, also see Hallé *et al.* 1978). A more programmed way to build additional crowns has been described under the name metamorphosis by Edelin (1984). Diagnostic criteria indicating the tree temperament can be expected to be found both in crown architecture and in tree canopy architecture with a particular arrangement of reiterated "crownlets".

It is to be understood from the outset that organs, shoots, branching patterns and reiteration patterns are all "adaptive tools", leading to a certain tree temperament. Between each of these features and each of the possible environments, there are no simple, straightforward and clear-cut relationships. In the overall biological efficiency of a tree in a certain environment, the combination of the features at different levels of organization is decisive. For leguminous trees, this has been analyzed by Oldeman (1988).

Unfortunately, this combination of features has not been studied thoroughly for any tree species, and certainly not over its whole life cycle. Insights can, however, be gleaned from piecing together published specialist information, complemented by unpublished data from Oldeman's field work files in French Guyana (1965–1974). The emerging image remains hypothetical but is falsifiable by observation and experimentation. No firmly proven tables or keys to tropical tree temperaments can be provided as yet for the forest manager.

A first review of published studies provides an overview of findings at the different system levels mentioned above. Thus, several attempts have been made to relate architectural models (Hallé and Oldeman 1970) and reiteration patterns (Oldeman 1974*a*, Hallé *et al.* 1978) to environments, as adaptive growth structures. Hallé *et al.* (1978) attempted to link them to K- and r-selected strategies, and Fournier (1979) tried to correlate models and specific biotopes. Only in exceptional cases could such correspondances be demonstrated clearly. For instance, Attims' model is particularly frequent

in trees of inundated forests, like mangroves, and rare in other environments, while Holttum's model clearly is geared to an r-strategy. Ashton (1978) and Givnish (1984) examined the problem from other angles, and found no conclusive evidence for clear-cut, immediate adaptive significance in the tree models described by Hallé and Oldeman (1970).

There is more convincing evidence for adaptive features at the hierarchical level of shoot architecture. Unbranched, monocaul trees, showing Corner's model, are well adapted to the forest undergrowth (Fournier 1979), and so is Cook's model which is morphologically different but physiognomically convergent (Hallé *et al.* 1978). The ecophysiologically derived hypothesis that multistemmed plants will be low in stature and single-stemmed plants will be tall (Givnish 1984) seems to hold true for temperate forest understoreys with their multistemmed shrubs, but not in the tropical rain forests where such shrubs are conspicuously rare. This difference cannot be explained as yet. In any case, monopodial, sparsely branched growth habits of many fast-growing tropical pioneer trees (see Whitmore, this volume) seem to enhance rapid height growth.

Continuous or intermittent growth of leader shoots in trees is well correlated with their successional status (Ashton 1978). Continuous growth is adaptive in uniform environments and rhythmic (intermittent) growth is adaptive in habitats with pronounced fluctuations in environmental conditions (Hallé *et al.* 1978, Fournier 1979). However, there is a complete range of intermediates (Fournier 1979, Lipman 1981).

That orthotropic axes are well adapted to sunny environments, and plagiotropic axes to shade is generally accepted (Hallé *et al.* 1978, Fournier 1979, Givnish 1984). Givnish has argued that: orthotropic axes favour height growth; erect axes can support more leaf mass per unit twig mass; plagiotropic branches or branch systems minimize self-shading, this being favourable for low-light photosynthesis near the compensation point; self-shading of leaves on orthotropic axes reduces transpiration losses in high-radiation environments.

The hypothesis that adaptation is easier to pinpoint at the level of shoot architecture than in whole tree architecture is strengthened by tree species displaying different architectural models in different environments (Kahn 1975, Hallé 1978). Such cases are rare in the tropics, however, and concern architectural models that resemble each other in organization. They differ most often by one structural differentiation only. For instance, a tree showing Leeuwenberg's model in the sun may replace it by Scarrone's model in the shade, substituting the terminally flowering orthotropic epicotyledonary axis by an indeterminate orthotropic shoot which functions as a perduring leader shoot. Again in trees conforming to Rauh's model, branches may be clearly orthotropic in the open and show some plagiotropic tendencies in the shade.

Fisher (1984, p. 580) aptly summarizes the conclusion in stating: "It appears that the architectural models of Hallé *et al.* (1978), are important for deterministic development, but a model *per se* need not be of adaptive significance. Crown shape, including branch and leaf geometry, is produced by the iteration of small scale elements and by the process of reiteration. Thus, seemingly small changes in the elemental parameters (branch angle, branch length) may have major effects on overall crown shape. What seems of major biological significance is the capacity for architectural change, i.e., plasticity. By this mechanism, a tree can respond opportunistically to changes in its environment".

Both tree architecture and shoot architecture therefore yield only partial answers in the quest for visible criteria for the diagnosis of tree temperament. Therefore, there is need to shift attention to the next lower level, that of the organs, where architectural features are considered like the means of support, supply and spatial arrangement of the organs. Photosynthetic organs that have been accorded special consideration include leaves and other photosynthetic units like phyllomorphs (cf. Hallé and Oldeman 1970) and short shoots (cf. Oldeman 1989). The key issue is the spatial arrangement of photosynthetic tissues, which is variously optimized so as to maximize assimilation in a tree under different environmental conditions.

Let us assume that, under given environmental circumstances, the leaf arrangement shown in Figure 2.2*a* is optimal. Several architectural models may now be apt to serve as "leaf carriers" providing the stems, branches and petioles needed to support the leaves and connect them with the roots (Fig. 2.2*b*). Physical and ecophysiological factors linked to the sap stream (Oldeman 1974*a*, 1990 in press) make certain architectural models more "economical" than others. This reduces the number of models once more (Fig. 2.2*c*). In this way, a leaf arrangement model can, in principle, predict the probability of one or a few well-defined leaf arrangements, each carried by a limited number of architectural models occurring under a given set of environmental conditions (also see the next section of this contribution). Such a model combines criteria at the three levels of organs, shoots and the architectural model, and hence is not strictly architectural.

Except for standard growth dynamics, conforming to tree models, this image is static. Such stereotypical growth patterns are an answer to rather constant climatic and soil conditions (Hallé and Oldeman 1970). But, during the life cycle of a tree, these conditions may change, sometimes in a drastic way. A tree should be adjusted optimally to a rather constant environment, or else have the capability to adjust rapidly to changing conditions. For abrupt increase of radiation or nutrient inputs, for instance, fast and "cheap" leaf formation might be implemented by either unbranched or rhythmically growing models (Fig. 2.2*d*). Reiteration of the model is a

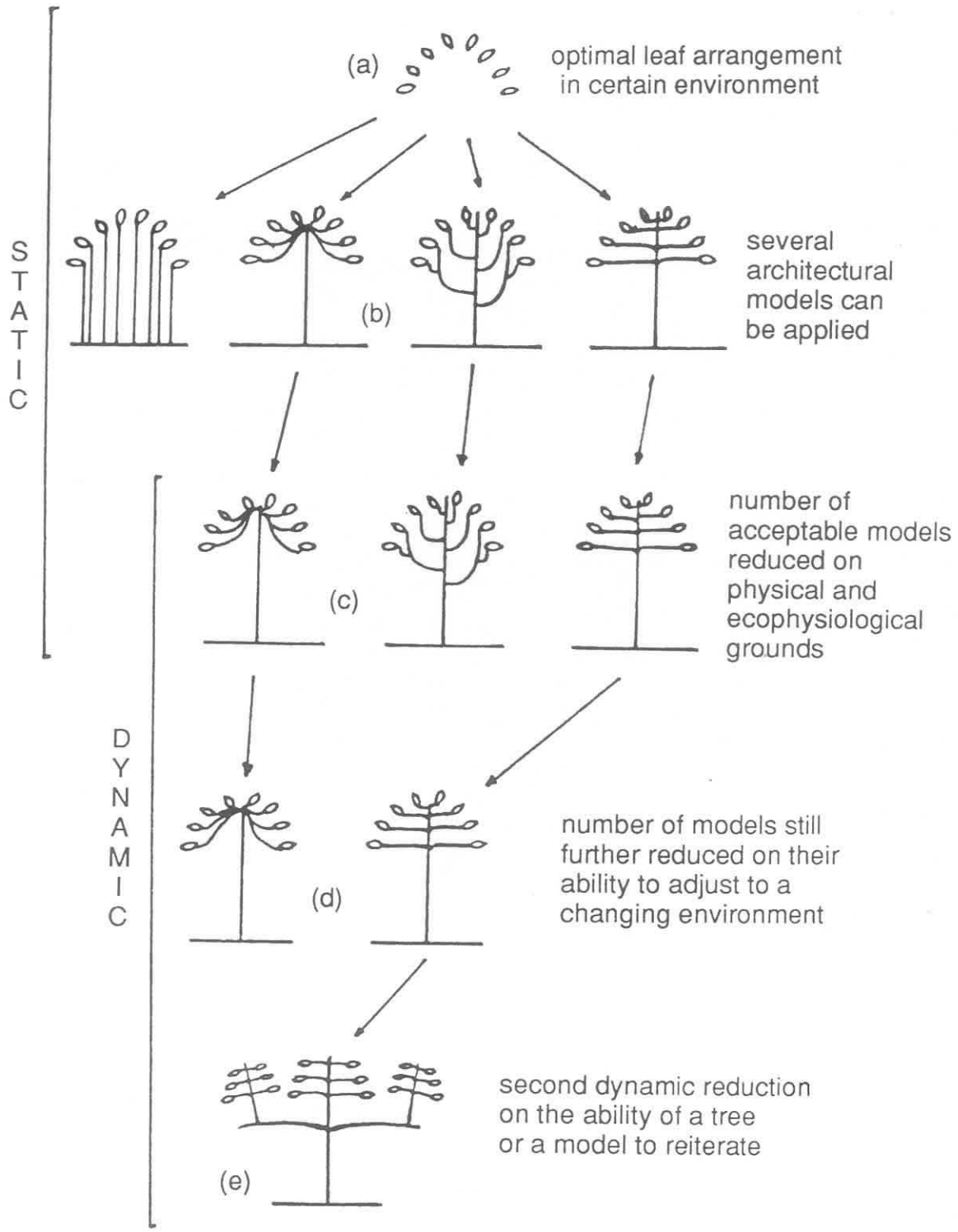


Fig. 2.2 Stepped selection of tree architecture as a support for adapted leaf arrangement. (a) Leaf canopy as needed, without support. (b) First selection of architectural tree models able to carry such a leaf arrangement. (c) to (e) Following steps of selection, models and trees without sufficient reiteration capacity being successively eliminated by the dynamic qualities of the immediate environment

particularly opportunistic mechanism (Hallé *et al.* 1978) and therefore the acme of flexibility is selected in the species that can reiterate rapidly and profusely (Fig. 2.2*e*). This selection mechanism is not to be seen apart from

the eco-unit determining the quality and quantity of radiation and nutrient inputs, as well as the selection pressure by competitors adapted to comparable environments.

The question might properly be posed as to what one can expect to gain by organizing the research needed to check this leaf arrangement model and its validity in the field, for selected tree species.

(1) Such a model should predict which tree is best adapted to a given sequence of environmental rain forest conditions encountered in its particular ecotope (see Oldeman 1974*b*, 1979, Hallé *et al.* 1978). However, not all tree species occupying the given ecotope will show a complete set of adaptive characters. Trees displaying the complete set will only be more frequent than less well-adapted species. Being optimally adapted is no guarantee that a tree will complete its life cycle and reproduce well enough to maintain its proportion of genes in the population: it only enhances its chances of doing so.

(2) The model should account for apparent but temporary low adaptiveness. Suppressed juvenile trees of canopy species may show little or no growth and seem ill-adapted when compared with other species that grow and reproduce in the same densely shaded undergrowth. However, such juveniles often respond quickly to the opening of the canopy, the quick response "over-ruling" the apparent imperfections of the suppressed state. In comparison with light-requiring seedlings and saplings of pioneer trees, survival ability under low light conditions for a sometimes considerable time is adaptive. Adaptiveness is a comparative notion.

(3) The model should allow comparison between tree performances. Intrinsic photosynthetic leaf properties may differ considerably. Hence, leaf arrangements that are apparently identical may be functionally different, adapting their trees to different environments (Ramakrishnan, this volume). However, if the photosynthetic performance is compared in two different leaf arrangements, both with a first type of leaves, their relative performance will not change if both are equipped with the same leaves again, but of a second type. In this sense, form reflects function.

(4) The model cannot be expected to cover all aspects of tree temperament. The leaf-arrangement model does not take root architecture into account. A measure of root architecture would certainly add to the performance of the model, but existing classifications of root shapes (e.g. Jeník 1978) are not formulated in a

way that allows them to be linked to above-ground architecture in a single architectural or functional model. The same is true for trunk models, even if centred around cambial functions.

It has been demonstrated above that no simple symptoms for tree temperament diagnosis are provided by the 23 architectural tree models (Hallé and Oldeman 1970). An improvement would be obtained by more detailed "architectural diagrams" (Edelin 1977), which add characters up to the specific level and so involve shoot and organ architecture in a more detailed way. This degree of precision is needed in autoecological studies, but it is costly and time-consuming to achieve in the species-rich tropical rain forest. Therefore, in the following paragraphs, particular architectural features are combined with other crown characteristics. The combination reflects the tree's environmental requirements and its flexibility in a changing environment. This attempt is again limited to visible, diagnostic features.

CROWN AND LEAF CHARACTERISTICS

Crown characteristics

Literature on crown characteristics is scarce. In the tropics, tree measurements have generally been restricted to the usual silvicultural parameters of height, diameter or girth at breast height, and clear bole height (crown depth). Moreover, these measures have nearly always been confined to trees > 10 cm diameter at breast height, leaving aside saplings and poles. Data on crown characteristics of young trees are scarcer still. As a consequence, the subject remains a largely hypothetical one (though the following section includes our own field data, in order to start checking the theoretical viewpoints proposed here).

The following discussion focusses successively on dicotyledons, monocotyledons and gymnosperms with emphasis on seedlings, saplings and poles. Mature tree crowns and reiteration will not be included.

Dicotyledons

Horn (1971) distinguished two basic leaf arrangements, monolayers and multilayers: in monolayers, leaves are densely packed in one single layer, while multilayers dispose their diffused leaves into many layers. Horn hypothesizes that multilayers are more productive in the sun, whereas monolayers produce more in the shade. Multilayers contain a far greater leaf surface than monolayers and, in open places, have so many leaves that, if spaced accurately, they are able to exceed monolayers in photosynthesizing performance at their light saturation rates. In the shade,

the leaves in monolayers can photosynthesize above their compensation points, whereas many of the lower leaves in multilayers will function below that point. Horn therefore predicts that early successional trees will tend towards multilayered leaf arrangements, and monolayers will occur in juvenile trees of late successional trees in the undergrowth.

Horn's predictions seem to apply quite well in temperate forests, but there are some obvious aberrations in tropical forests – with their great variety of life forms. The first are sparsely branched, large-leaved, nearly monolayered pioneer trees, such as *Cecropia* spp., *Musanga cecropiodes* or *Macaranga gigantea*, from the neotropics, tropical Africa and tropical Asia, respectively. They seem to be adapted exclusively to rapid height growth without "wasting" biomass to build multilayered leaf arrangements. Large leaves on "cheap" petioles serve as throw-away photosynthetic units and the trees can put most photosynthates into the growth of a single shoot (Coombe and Hadfield 1962, Bazzaz and Pickett 1980, Givnish 1984).

Another aberration from Horn's predictions is the "pauci-layer". This pagoda tree, in which leaves are disposed in a limited number of distinct layers is exemplified in genera such as the pantropical *Terminalia* or the palaeotropical *Alstonia*. These "pagoda" trees (Corner 1952) are very flexible, can be found among both pioneers and emergents (Pickett 1983) and are distinctive for later seral succession (Ashton 1978, Unesco 1978). Their branches show plagiotropy by apposition (Hallé and Oldeman 1970), are adaptive in the shade, in combination with a single orthotropic leader shoot, which grows rapidly in height (Ashton 1978). Several architectural models may be shown by pagoda trees (Fisher 1978, Hallé *et al.* 1978), but Aubréville's model, in which the leaves are most evenly spaced within each branch tier (Hallé *et al.* 1978), seems to be the most frequent and successful one (Kahn 1975).

A third aberration from Horn's predictions is represented by suppressed juveniles of canopy trees, waiting for a canopy gap in which to grow, and which have tall and narrow crowns (Hallé *et al.* 1978, Bruenig 1983) with a high leaf area index. Hence, these trees are essentially multilayers.

To extend the validity of Horn's temperate model to the tropics, Givnish (1984) substituted the "ecological compensation point of a leaf" for Horn's "photosynthetic compensation point". Givnish added six cost items in terms of energy. The leaf arrangement of a tree represents a certain balance amongst these cost items, in summary:

(1) nightly leaf respiration,

(2) cost of leaf construction,

(3) cost of root, xylem and phloem building and maintenance,

(4) cost of tissues supporting leaves,

(5) losses due to herbivory or diseases,

(6) cost of nutrient extraction and displacement from shaded leaves towards young, well-lit leaves. We add a seventh item, i.e.

(7) cost of strategic investment.

This cost is illustrated by a juvenile tree building and maintaining a multilayered leaf arrangement in the shaded undergrowth, which only becomes an energetic advantage instead of a drawback when the canopy opens and it helps the tree to outgrow its competitors.

Monocotyledons

Palms are by far the most prominent tropical monocots. Many are found in dynamic forests, in which new eco-units are frequently opened up by wind, unstable soils or flooding (Givnish 1978, de Granville 1978, 1984, Oldeman 1990, in press). Palms contain many efficient "gap colonists" with single erect axes and large compound leaves as throw-away photosynthesizers. Givnish (1978) hypothesizes that "feather palms" with long, pinnate fronds are colonists of small eco-units ("gaps") and "fan palms" with shorter palmate fronds tend to colonize large new eco-units.

He argues that the compact, (hemi-) spherical crowns of fan palms are vulnerable to overtopping and shading that menace them in small eco-units. Fan palms moreover have a high degree of self-shading, minimizing transpiration losses in sunny or dry habits. In contrast, the umbrella-shaped crowns of feather palms (Hallé *et al.* 1978) are, according to Givnish, much less vulnerable to overtopping and shading, while long pinnate fronds minimize self-shading. De Granville (1978) adds the function of funnel-shaped palm crowns in the understorey of tropical American rain forests as "litter collectors", concentrating litter masses at the foot of the palm. This function also fits in small eco-units, which are exposed to litter falling from nearby trees.

Givnish's hypothesis is supported by amphistomaty, characteristic of light-requiring plants (Parkhurst 1980, ex Givnish 1984) and being frequent in fan palms, whereas most feather palms are hypostomatous (Tomlinson 1961, ex Givnish 1984). Other, non-monocotyledonous trees such as *Araliaceae* species and tree ferns show leaf arrangements similar to feather palms and are colonists of rather small gaps at higher altitudes in the tropics (Givnish 1978, 1984). De Granville (1978) drew attention to palm habitats being more frequently filled by tree ferns with increasing altitude. The pioneer tree ferns of the Antilles and the high Andes seem to be an exception to this rule-of-thumb.

Quite a few short-stemmed or stemless palms are characteristic of the rain forest understorey in tropical America and Asia. They most often have funnel-shaped crowns, but flattened disks also occur (Hallé *et al.* 1978, de

Granville 1978). Some understorey palms, like the Asian *Eugeissonia tristis* or American *Astrocaryum* species form dense, monolayered thickets virtually blocking the germination and establishment of other plants (Ashton 1978, Dransfield 1978, de Granville 1978, Kahn 1986).

Gymnosperms

Many conifers conform to their archictectural model throughout their life cycle, showing little or no reiteration (Hallé *et al.* 1978; but see Edelin 1977). Their strongly monopodial growth habit results in characteristic narrow and elongate, cylindrical or conical crowns (Whitmore 1975). Most conifers are heliophilous and act either like small eco-unit dwellers (e.g. *Agathis* and *Araucaria* species), or large eco-unit colonizers (e.g. *Pinus* species; Whitmore 1975, Denslow 1980). In terms of available light, this almost certainly means that many newly formed, small, but narrow eco-units in high forest are lethal environments for tropical gymnosperms. Probably, these latter tropical conifers are all multilayers, as was found by Horn (1971) for all temperate coniferous gap species, such as *Pinus* and *Sequoia* species.

Leaf characteristics

At a more detailed level of the organs being carried by the crowns, Givnish (1984) has provided an excellent review of leaf characteristics and their ecological significance, the most relevant conclusions of which are summarized here.

Leaf size

Many authors have observed decreases in leaf size towards sunny, dry or nutrient-poor sites. Indeed, the mathematical model of Givnish and Vermeij (1976), which calculates differences between photosynthetic gains and transpiration costs, predicts that the smallest leaves will be found in xeric, sunny environments. In moist, shaded rain forest understoreys, leaf size is not very adaptive and so a wide range of leaf sizes may be expected there (Givnish and Vermeij 1976, Chiariello 1984). Tropical forest trees may indeed often have large juvenile leaves and much smaller adult ones (e.g. *Shorea curtisii*, Ashton 1978), as has been mentioned in rain forest literature since the beginning of the century (e.g. Schimper 1903). The large, simple leaves of many pioneer tree species may be an energetically cheap solution for adapting trees to rapid height growth.

Compound leaves

Givnish (1978) argues that deciduous compound leaves reduce costs in warm, arid habitats, the shedding of highest-order branches or large

rachises minimizing transpiration losses. Their ecological signifiance in early successional trees has been discussed above.

Leaf inclination

Trees with peripheral leaves or leaflets steeply inclined with respect to the horizontal plane are noticeable in sunny, dry or nutrient-poor habitats. Such inclination reduces heat load and consequently also transpiration of the outer leaves. It may also increase the potential leaf area index of a crown, light penetrating more deeply into it, which is quite important for multilayer arrangements. Indeed, Ashton (1978) found that trees with leaves oriented more perpendicularly to incident light tend to have relatively low leaf area indices.

The leaf characters mentioned above can be seen immediately and are therefore diagnostic. Other characteristics fall beyond the scope of this contribution. Leaf translocation and leaf turnover rates, for instance, are of prime importance in nutrient turnover and conservation (cf. Ramakrishnan this volume), but they have to be measured and cannot be seen directly in the field, except by linking them to visible architectural symptoms, as has been done by Givnish. Other intrinsic but invisible properties of leaves are, for instance, leaf production and longevity (Bazzaz and Pickett 1980, Bazzaz 1984); deciduousness (Givnish 1978, 1984, Medina 1983, Carabias-Lillo and Guevara Sada 1985); palatability (Hartshorn 1978, 1980, Hladik 1978); autotoxicity; reflectivity (Givnish 1984); thickness and consistency; indument; and still more hidden physiological properties (e.g. Bazzaz and Pickett 1980, Mooney *et al.* 1984).

LIFE HISTORY TYPES AND REGENERATION STRATEGIES

As noted in the introduction, foresters have for several centuries recognized different life histories of forest trees, distinguishing at least three "temperaments" in light-demanding (heliophilous), half-tolerant and shade-tolerant (sciadophilous) trees (for definitions, see Mayer 1980; for a critical review, Lanier 1986).

Trees living and reproducing in the dense shade of the forest understorey (not distinguished in classical forestry);

Trees living and reproducing in the understorey but benefiting from light gaps; (would be very tolerant trees in forestry; "Schattbaumarten", see Mayer 1980);

Trees with juvenile establishment in the shaded understorey and

needing a gap to grow up and mature (classical shade-tolerant trees in forestry; "Schattbaumarten", see Mayer 1980);

Trees that become established and grow up in gaps (light-demanding trees in forestry; "Lichtbaumarten", see Mayer 1980).

Trees that tolerate medium to light shade when establishing themselves and that need gaps to grow up and mature (half-tolerant; "Halbschattbaumarten", see Mayer 1980).

And recently, a temperament that had dropped out of forestry manuals with the decreased interest in coppice-with-standards, a traditional European system of farm silviculture, was rediscovered in the tropics. The word "late-tolerant" was coined to name this temperament (Oldeman 1990, in press).

Trees that germinate, that become established and mature in the light of gaps and that survive a long time in the shade of later-overtopping larger trees.

Kahn (1982) described *Microdesmis puberula* and *Myrianthus liberica* in Côte d'Ivoire. They display this late-tolerant temperament. These species can form a mature understorey (structural set, Hallé *et al.* 1978) below a canopy of overtopping pioneer trees. Some *Inga* species in French Guyana may do the same (Poncy 1985, Lescure 1986). In Mexico and Central America, *Piper amalago* and other *Piper* species exemplify this temperament (Gómez-Pompa *pers. comm.*, 1986). In the case of *M. puberula*, *M. liberica* and *Inga* spp., these small trees have been followed through successive steps of their establishment and growth. They have certainly not originated from tolerant seedlings.

During the last decade, such life history types have been linked to eco-unit size in the forest ecosystem (e.g. Hartshorn 1978, 1980, Oldeman 1978, 1983, 1987, Whitmore 1978, Denslow 1980, Brokaw 1985, Vooren 1986). Tolerant trees do best in small eco-units, created by the fall of a single tree. Intermediate eco-units and border zones of eco-units would yield good early environments for semi-tolerant trees. And light-demanding or late-tolerant species need gaps of about 200 m^2 or more. Denslow (1980) therefore distinguished small-gap specialists (shade-tolerant) and large-gap specialists (light-demanding, late-tolerant).

Life history types is a notion associated with the vegetative development of individual trees. In terms of species, i.e. populations, it is also important to consider reproductive strategies. Following Bazzaz and Pickett (1980) and Pickett (1983), contrasting "gambler" and "struggler" strategies can be distinguished. Species with a gambler strategy produce numerous seedlings

which are unable to survive in the shaded understorey of old eco-units and which need light in young, larger eco-units where they may grow rapidly. Gamblers expend massive efforts in reproduction and thus the chances are high that at least one juvenile tree per effort will become established in a suitable young eco-unit.

Species with a struggler strategy produce few, very persistent seedlings, which struggle but survive and show some growth in the densely shaded understorey. Some can even complete their life cycles there. Reproductive efforts of strugglers are effective at low intensities, while the life expectancy of each juvenile is higher.

The struggler-versus-gambler model of Bazzaz and Pickett (1980) is an updated and modified version of van Steenis' (1958) nomad-versus-dryad concept. The new version is a step forward in that it links the van Steenis view to other biological population models in such a way that it can be expressed numerically. This issue can be placed easily in the context of the discussion on r- and K-selection, a notion which is akin to the concepts mentioned here, (cf. Begon *et al.* 1986, their chapter 14).

It is useful to visualize the result of the "gambler" and "struggler" strategies in terms of eco-unit development. In Figure 2.3, these abstract considerations are translated into an image of the kind of patterns in a tree population that may be observed in the field, when observing different developmental phases of an eco-unit. Scale-drawings of real situations, depicting such observed developments, have been at the base of the rediscovery of late-tolerant species by Kahn (1982) and Lescure (1986). It is useful to realize that the gambler strategy works best in large young eco-units, where not only the germination environment is exposed to high light intensities, but these conditions persist throughout the life of the tree. In contrast, the struggler strategy is most suited to the successive opening of small to very small eco-units, or even temporary damage to the canopy of a persisting eco-unit, because it allows a resumption of height growth with each successive modest increase in light.

A more comprehensive classification of juvenile tree temperaments may be reached by combining their vegetative life history, according to criteria found at different levels and discussed above, and their reproductive strategy. An analogous effort for all Mexican plant types in the Veracruz rain forest has been visualized schematically by Gómez-Pompa and Vázquez-Yanes (1985). In the following list of tropical forest tree temperaments, the reproductive strategy has been used to define extremes, i.e. hard strugglers and hard gamblers. Between these extremes, intermediate temperaments depend very much upon crown and leaf characteristics.

(1) Hard strugglers. Offspring are produced infrequently in low numbers.

Crown and leaf characteristics enable completion of the whole life cycle in dense shade within older forest eco-units with a closed canopy. Shade tolerance remains high during the life cycle. Increased light levels may be beneficial but are not indispensable, whereas abrupt exposure to high light intensity is lethal.

(2) Strugglers. Offspring are produced infrequently in low numbers. Crown and leaf characteristics are flexible, permitting a development from shade-tolerant seedlings to later development stages that are less tolerant, whether they grow up into the upper canopy or not. Abrupt exposure to full sunlight is often detrimental.

(3a) Gambling strugglers. Offspring are produced frequently in high numbers. This is a characteristic of gambling strategies though crown and leaf characteristics show much of the struggler temperament. From the shade-tolerant seedling – which, however, demands a light intensity steadily increasing with height from the ground – gambling strugglers grow very fast. Later they can be overtopped by larger trees and complete their life cycle as strugglers under the canopy.

(3b) Struggling gamblers. Offspring are produced frequently in high numbers. Crown and leaf characteristics are flexible, but, from the shade-tolerant seedling, juveniles soon pass into a phase of light-demanding development which is irreversible. Hence, they can only complete their life cycle in the upper canopy of a mature eco-unit (see Fig. 2.1); if overtopped, they die.

(4a) Gamblers. Offspring are produced frequently in high numbers. Crown and leaf characteristics are so flexible that the trees, which arise from seedlings and juveniles that tolerate no shade at all, can later survive under a certain amount of shade. The difference with gambling strugglers is not only in the light tolerance of the seedling, but also in crown and leaf characteristics that are not especially adapted to live in the shade, but flexible enough to accommodate some shade.

(4b) Hard gamblers. Offspring are produced frequently in vast numbers. Given their leaf and crown characteristics, from the seedling on, these trees can only survive and grow in full light throughout their life cycle. This condition is to be found mainly in large-sized young eco-units with little remaining vegetation, and maintained only for those individual trees that grow ahead of the dense population as a whole (Fig. 2.3).

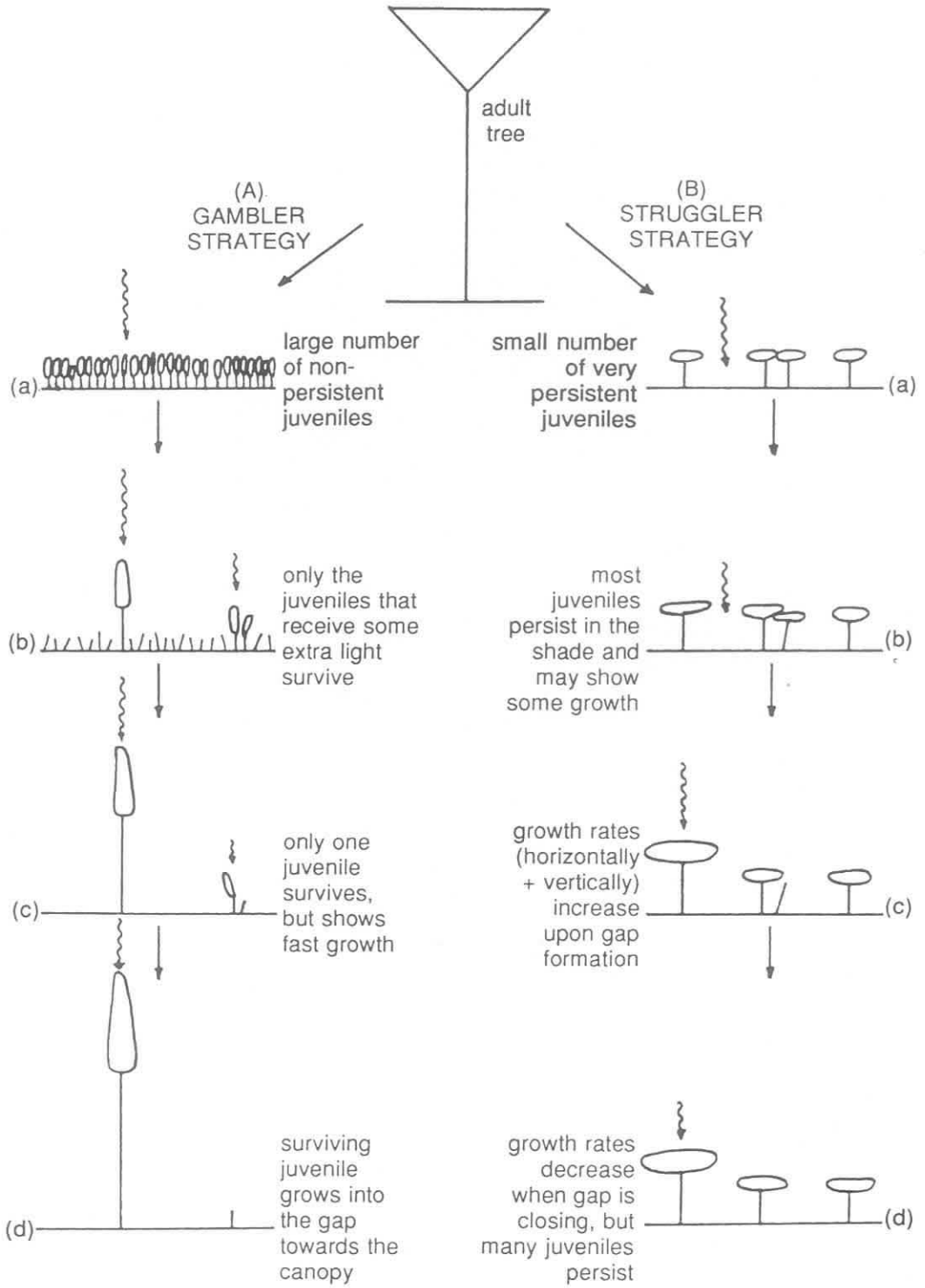

adult tree
(A) GAMBLER STRATEGY
(B) STRUGGLER STRATEGY
(a)
large number of non-persistent juveniles
small number of very persistent juveniles
(a)
(b)
only the juveniles that receive some extra light survive
most juveniles persist in the shade and may show some growth
(b)
(c)
only one juvenile survives, but shows fast growth
growth rates (horizontally + vertically) increase upon gap formation
(c)
(d)
surviving juvenile grows into the gap towards the canopy
growth rates decrease when gap is closing, but many juveniles persist
(d)

Fig. 2.3 Visualization of two extreme reproduction strategies, geared to be successful in different eco-units (Figs. 2.1 and 2.9). A – Hard gamblers saturate large and sunny young eco-units (cf. Fig. 2.9, to the right of the middle) with diaspores, survival and further growth demanding light and depending on crown characteristics (Table 2.5). B – Hard strugglers produce few diaspores in closed, older eco-units (Fig. 2.1C), survival and further growth tolerating quite heavy shade, being vulnerable to abrupt increases of light, and depending on crown characteristics (Table 2.5). Undulating arrows: incident solar radiation, length indicating intensity. (a) to (d) show population development during development of the eco-units, the hard gamblers becoming most often overtopped so that few survivors are left, and the hard strugglers maintaining a small but rather constant population as long as no major disturbance destroys the "mature" eco-unit in which they live

Light is the environmental factor appearing in each description of a temperament. As already noted, foresters have long recognized the major importance of this factor in the definition of temperaments, and Whitmore (1975, this volume) gives thorough descriptions of the two extreme temperaments that were distinguished. Light-demanding trees or pioneers, colonizing large open terrains, have long been known for their combination of special crown and leaf characteristics, their fast growth and often short life span, and their abundant seed production.

But is there only one category of non-pioneers? Given the many variations on the theme of eco-unit development as schematically shown in Figure 2.1 – characterized by different sizes and shapes, different development and growth rates, and different species compositions (including that of species other than trees) – those trees which are not pioneers may encounter all kinds of sequences of light and shade during their lifetime. If the pioneer displays an extreme temperament, the other extreme is not the non-pioneer but rather the anti-pioneer, for which intensive light is lethal. Pioneers are characterized by the temperament described here as "hard gamblers" and anti-pioneers as "hard strugglers". The other four temperaments mentioned above are intermediates. Their descriptions with the recurrent reference to flexibility already point to the fact that they do not concern discrete categories, but are landmarks in what may well be a continuum of environmental conditions, some of which are more frequent and more easily observed in the forest than others.

Figure 2.4 shows the ecological setting for these six tree temperament landmarks. They are clearly linked to the size of the eco-unit concerned (Oldeman 1983), because large eco-units are high-radiation environments from the outset and small eco-units show intermediate to low light intensities at ground level at the start of their development. But these strategies are also linked to eco-unit development and architecture (Fig. 2.1A to D). This is the time dimension in Figure 2.4, from young below to mature above. In different eco-unit development sequences, different shifts in temperament of a tree species enhance survival. The importance of the seedling and juvenile stages, as the time interval during which such shifts occur, is clear, and the neglect of this period in most classical silvicultural temperament studies can therefore be recognized for the handicap it is.

The vertical axis in Figure 2.4 also has a spatial connotation. Because temperaments are defined by crown and leaf characteristics and by reproductive strategies, the lower reaches of the figure concern the undergrowth, and the upper parts indicate the potential or the real upper crown canopy level of the eco-unit concerned. Because there is a gradual increase in light intensity from forest floor to forest canopy, also in eco-units, struggling for light is less intense higher up in an eco-unit than lower down. The hard strugglers therefore are indeed struggling more than struggling gamblers and gambling strugglers (Fig. 2.4).

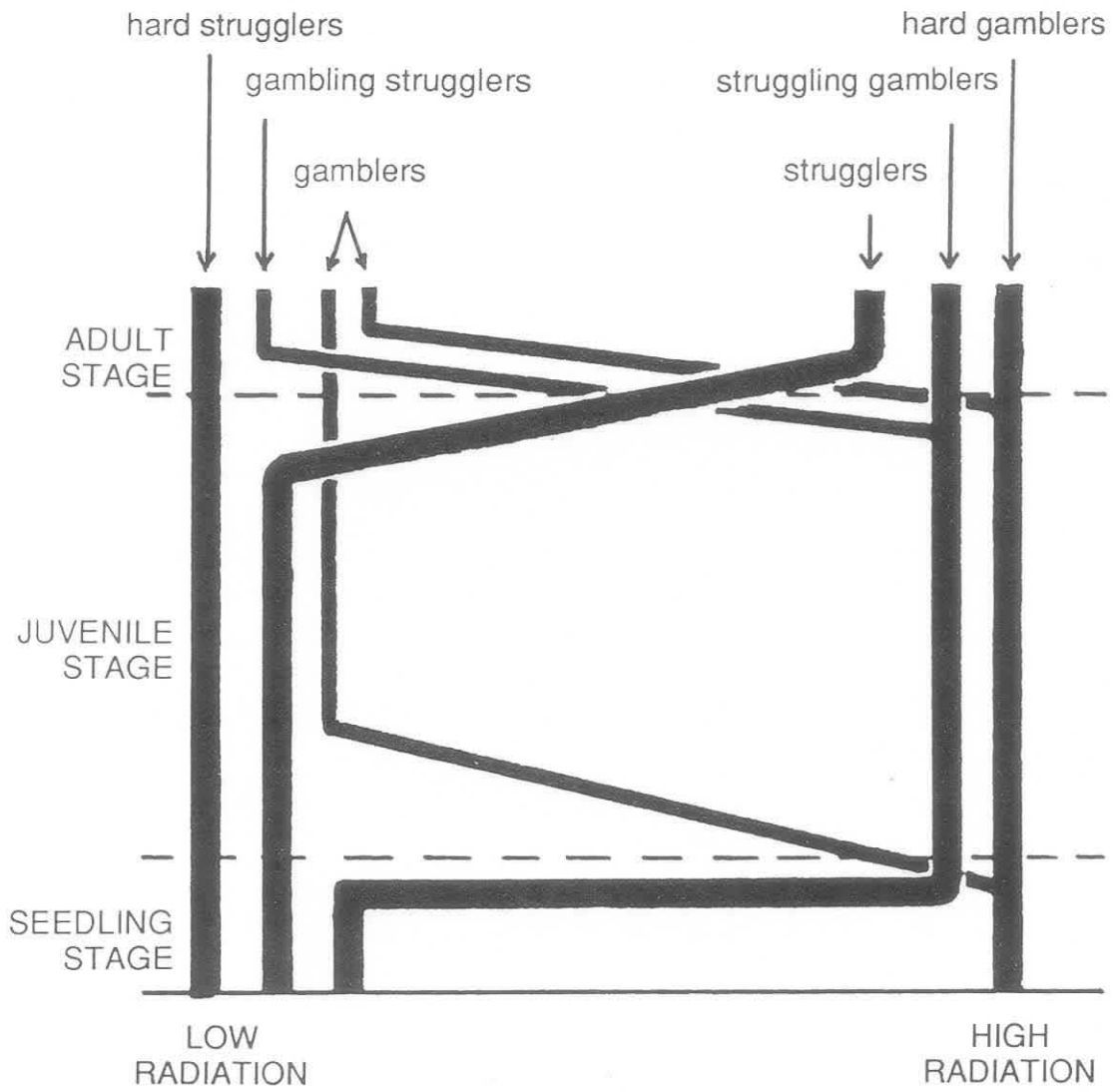


Fig. 2.4 Visualization of six tree temperaments. Each temperament may either remain constant from seedling to adult tree (hard strugglers, hard gamblers), or be flexible and change its shade tolerance at some stage of the life cycle (others). The vertical dimension of this diagram evaluates height above ground level, which will be different for each tree species. It also refers to processes, but the tempo and rhythm of these processes differ for each tree species, and thus this is also a relative scaling. The strugglers closely correspond to the classical "shade-bearers" or "climax species", the hard gamblers to classical "light-demanding" or "pioneer" species. The relative frequency of a temperament is indicated by the thickness of the bar

The figure would be compatible with a continuum of temperaments, on which the frequent ones have been indicated schematically. This frequency is determined by the most regularly occurring geometrical and dynamic patterns in eco-unit development, determining the immediate environment of the tree and its ecological properties. The continuum, therefore, is not homogeneous, in which case it would be sufficient to characterize the extreme strategies in the sense of van Steenis (1958) as "nomads" and "dryads". Neither is its heterogeneity determined exclusively by eco-unit (gap) size as a geometrical parameter, so that the simple division in "small

and large gap specialists" (Denslow 1980) also is an oversimplification. Temperaments of tree species have to contain reactions to factors determined by both geometry and dynamics of forest development, and therefore the frequent strategies in Figure 2.4 are closely linked to eco-unit development (Fig. 2.1).

Some data from the literature confirm the danger of oversimplification in exclusive categories such as "pioneers" versus "non-pioneers", "nomads" versus "dryads" or "light-requiring" versus "shade-tolerant" tree species. Vázquez-Yanes and Orozco-Segovia (1985) drew attention to the necessary increase in the red/far-red ratio of the spectrum, if maximum light intensity is to trigger pioneer germination. Florence (1981) found that pioneer seeds in Gabon germinate in light intensities below full exposure. For instance, *Musanga cecropioides* could germinate in eco-unit border zones with light intensities between 40% and 80% of full sunlight. This fact has been established experimentally for *Cecropia surinamensis* seeds from Suriname by Holthuijzen and Boerboom (1982). The seedling phase alone, therefore, takes place in a very complex environment, be it shaded or not, and studies that combine the quantitative and qualitative aspects of radiation in this environment seem to be very rare.

Figure 2.4 is admittedly not comprehensive, because some rarer strategies are not shown, e.g. the "sciaphilous nomads" (Oldeman 1974*a*, Hallé *et al.* 1978) which grow in "ecological chimneys" with a slow and small intensive vertical light gradient. However, it does indicate the most frequently encountered tree species strategies – recognizable in the juvenile stage by visible characters of crown and branch architecture and leaf arrangement.

Hard strugglers (1) are found in older eco-units under closed canopy (Fig. 2.1B and C). Their crowns are monolayered and more broad than deep. Leaves are borne on plagiotropic branches or, in monocaul trees, in a whorl just below the stem apex. Growth may be mainly horizontal, but also vertical when gap formation slightly increases light availability (cf. Hartshorn 1980).

Strugglers, gambling strugglers and struggling gamblers (2 and 3) are taken together here, because studies are as yet lacking on representative species which are precise enough to order the visible characteristics of each with sufficient confidence. These temperaments often occur in large, economically important trees. For example, many South-east Asian Dipterocarpaceae may be regarded as being shade-tolerant or even needing shade during part of their life cycle. In this family of large trees, shade-bearers and light-demanding species can be recognized readily (cf. Whitmore 1975, his references). Among the strugglers are slow-growing, shade-tolerant "heavy hardwoods", e.g. the balau group of *Shorea* and species of *Vatica*, *Hopea* or *Neobalanocarpus heimii*. Struggling gamblers are to be found among the light-demanding "light hardwoods" which

require shade only during the first life phases and later grow very fast in high radiation environments, such as the red meranti group in *Shorea*, or species of *Parashorea* and *Dipterocarpus*. The need for shade before canopy closure is reflected in the observation that high soil temperatures are lethal for the quite specific mycorrhizal fungi that are associated with these dipterocarps in Kalimantan (Smits *et al.* 1987). This is yet another indication that temperaments are no simple categories linked to light requirements or gap sizes, but result from complex strategies adapted to eco-unit development.

The architecture of all canopy trees favours rapid height growth, allowing them to reach the canopy quickly. Monopodial growth is therefore beneficial, shade tolerance being visible by plagiotropic branch orientation, pointing to a struggler metabolism. Orthotropic axes rather favour gamblers. The nec-plus-ultra in architectural flexibility is attained in the Leguminosae (Oldeman 1988), where, in a single species, axes and branched complexes are capable of either struggler or gambler behaviour, depending on the ambient environment. Leguminosae with sympodial growth models dominate the high canopy tree flora of the tropical American and African rain forests. These tree species most often have plagiotropic mixed axes, being capable of either horizontal or vertical extension.

Leaf arrangement may tend to be monolayered in strugglers and multilayered in gamblers. Families like the Dipterocarpaceae have clear-cut architectures in this sense, whereas Leguminosae represent the other extreme of being able to build the two arrangements, both in the same species and in different development periods of the same tree.

Gamblers and hard gamblers (4) are adapted to continuously high radiation levels and do not support shade. Their survival depends upon outgrowing their competitors. This is made possible by the well-known characteristic architecture of pioneer trees, growing in very large eco-units. Their single leader shoot is usually sparsely or not branched and bears large leaves in a single, subapical layer. Such monolayers may not be most productive in terms of photosynthesis, multilayers being more productive in smaller gaps (see above), but they certainly are most competitive in placing their entire crowns above their competitors (Ashton 1978).

However, tree components of large eco-units do exist that build multilayered leaf arrangements. Examples are *Macaranga hypoleuca* from tropical Asia (Ashton 1978), *Goupia glabra* and *Ceiba pentandra* in tropical America (see section below) and some tropical conifers (Whitmore 1975). It may be relevant that, among such pioneers, there are long-lived and very large trees, as is the case in *G. glabra* and *C. pentandra* (see also the paragraphs on emergents in Hallé *et al.* 1978). According to Oldeman (1990, in press), they may be termed long-lived pioneers and play a predominant role in the fragmentation of large eco-units into small eco-units.

A FIRST STEP TOWARDS FIELD CHECKS

As stated above, the proposed hypotheses cannot be validated as yet from literature. Therefore, use was made of an unpublished file by Oldeman, containing data on over a hundred tree and shrub species from French Guyana in the form of drawings, slides, photographs and notes. This information mostly concerned juvenile plants, and has been gathered between 1965 and 1974. We processed the information on those species for which the data were sufficient for a first check of their strategy and environment.

Tables 2.1 to 2.4 summarize important architectural features for each species, to which is attached one of the temperaments above. The first column gives the architectural model (Hallé and Oldeman 1970), the second the maximum attainable height, if known. In the third column, the mode of height growth is given as monopodial or sympodial, and the fourth column provides information on branch orientation (either plagiotropic or orthotropic). In the last column, branching is characterized as rhythmical (intermittent) or continuous, this last term includes diffuse branching with no discernible pattern of intermittence.

The files only contained a few miscellaneous notes on the eco-units in which the trees were observed. Therefore, the tables do not give any

Table 2.1 Hard strugglers and strugglers from French Guyana. These are small, monolayer trees from the understorey of the tropical rain forest, with a simple architecture. From Oldeman (unpub.)

Species	*Arch.*[1] *model*	*Height*[2] *max.(m)*	*Height*[3] *growth*	*Branch*[4] *orient*	*Branching sequence*
Carica cf. spec.nov.	CORNE	2	mono	.....	.....
Casearia bracteifa	ROUX	2	mono	plagio	diffuse
Cedrela cf. *barbata*	CHAMB	–	sym	.....	.....
Geonoma stricta	TOMLI	1	mono	.....	.....
Guarea richardiana	CORNE	2	mono	.....	.....
Pavonia cf. *flavispina*	CHAMB	0.5	sym	.....	.....
Picrolemma cf. *pseudocoffea*	CHAMB	(1.5)	sym	.....	.....
Quiina oyapocensis var. *bicolor*	CHAMB	–	sym	.....	.....
Ryania speciosa	COOK	(7)	mono	plagio	diffuse
Talisia mollis	CHAMB	(6)	sym	.....	.....

LEGEND – = not known; ..... = undefined or not applicable

Column (1) – AUBRE = Aubréville's model; CHAMB = Chamberlain's model; COOK = Cook's model; CORNE = Corner's model; FAGER = Fagerlind's model; KORIB = Koriba's model; LEEUW = Leeuwenberg's model; MANGE = Mangenot's model; MASSA = Massart's model; NOZER = Nozeran's model; PETIT = Petit's model; PREVO = Prévost's model; RAUH = Rauh's model; ROUX = Roux's model; TOMLI = Tomlinson's model; TROLL = Troll's model.
Column (2) – numbers in parentheses are not the maximum heights observed for the species, but the heights of the actual trees in the file (Oldeman, unpub.).
Column (3) – mono = monopodial; sym = sympodial
Column (4) – plagio = plagiotropic; ortho = orthotropic

Table 2.2 Hard strugglers and strugglers from French Guyana. These are trees between 6 and 18 m high, from the lower reaches of the tropical rain forest. Their crown characteristics are a little more complex than in small strugglers and leaves are diffuse throughout the crown. Legend: See Table 2.1. From Oldeman (unpub.)

Species	*Arch.*[1] *model*	*Height*[2] *max.* (m)	*Height*[3] *growth*	*Branch*[4] *orient*	*Branching sequence*
Anaxgorea acuminata	TROLL	6	sym	plagio	.....
Byrsonima verbascifolia	FAGER	–	mono	plagio	inter
Couepia cf. *versicolor*	TROLL	(4)	sym	plagio	.....
Dugutia cf. *obovata*	ROUX	12	mono	plagio	diffuse
Guatteria cf. *ouregou*	ROUX	–	mono	plagio	diffuse
Himatanthus articulatus	KORIB	12	sym	ortho	.....
Hirtella velutina	TROLL	–	sym	plagio	.....
Licania aff. *ovalifolia*	TROLL	–	sym	plagio	.....
Miconia plukenetii	LEEUW	12	sym	ortho	.....
Mouriri frankavillana	MANGE	12+	sym	plagio	.....
Perebea guianensis	ROUX	15	mono	plagio	diffuse
Quararibea turbinata	FAGER	17	mono	plagio	inter
Tachigalia spp.	PETIT	6	mono	plagio	diffuse

Table 2.3 Struggling gamblers, gambling strugglers and a few higher strugglers from French Guyana. These are trees able to form an upper forest canopy, which grow up in small eco-units having resulted from small gaps. Their crown characteristics are more complex and leaves occur in pauci-layers or pagoda-like arrrangements. Legend: See Table 2.1. From Oldeman (unpub.)

Species	*Arch.*[1] *model*	*Height*[2] *max.* (m)	*Height*[3] *growth*	*Branch*[4] *orient*	*Branching sequence*
Aniba sp.	RAUH	–	mono	ortho	inter
Aparisthmium cordatum	KORIB	25	sym	ortho	.....
Aspidosperma sp.	MASSA	'large'	mono	plagio	inter
Cordia spp.	PREVO	–	sym	ortho	.....
Diospyros sp.	MASSA	25+	mono	plagio	inter
Eriotheca sp.	RAUH	'large'	mono	ortho	inter
Iryanthera hostmanii	MASSA	25	mono	plagio	inter
Manilkara bidentata	AUBRE	'large'	mono	plagio	inter
Ocotea splendens	MASSA	–	mono	plagio	inter
Pourouma minor	AUBRE	15+	mono	plagio	inter
Tetragastris altissima	RAUH	'large'	mono	ortho	inter
Theobroma speciosum	NOZER	30	sym	plagio	.....

reference to a temperament per tree species. In each successive table, a group of species has been placed in a certain height category. Among these trees, different temperaments are present, and these will be discussed below. The result of this discussion is illustrated by Figures 2.5 to 2.8. The image that emerges is coherent and supports the existence of a series of temperaments, from hard gamblers to hard strugglers, with intermediates.

Table 2.4 Hard gamblers and gamblers from French Guyana. These are trees that form a low or a high forest canopy in large clearings and deforested areas and often form huge eco-units, which may live only a short time. Their crown characteristics are quite diverse (also see figures and Table 2.5). Legend: see Table 2.1. From Oldeman (unpub.)

Species	*Arch.*[1] *model*	*Height*[2] *max.*(m)	*Height*[3] *growth*	*Branch*[4] *orient*	*Branching sequence*
Annona paludosa	TROLL	–	mono	plagio	.....
Apeiba burchelli	TROLL	15	mono	plagio	.....
Ceiba pentandra	MASSA	50+	mono	plagio	inter
Didymopanax morototoni	LEEUW	20+	mono sym	ortho	.....
Goupia glabra	ROUX	50+	mono	plagio	diffuse
Jacaranda copaia	CHAMB LEEUW	15+	sym	ortho	.....
Toulicia guianensis	LEEUW	30	mono sym	ortho	.....

Hard strugglers

Hard strugglers all occur in the understorey, with a maximum height of around 15 m. A group of small, monolayered trees mostly much under 10 m (Table 2.1) is distinguished from a group of larger trees with more complex crown characteristics that may reach a height of 10 to 15 m (Table 2.2).

In the first group, there are 10 examples (Table 2.1). Most display a monocaul habit, built sympodially (Chamberlain's model) or monopodially (Corner's model), with a few large, simple or compound leaves at the top. *Geonoma stricta* (Palmae, Tomlinson's model) can be considered as a cluster of such monocaul trees. The two branched species remain functionally close to the monocauls. *Ryania speciosa* var. *bicolor*, with its phyllomorphic branches, conforms to Cook's model, whereas *Casearia bracteifera* shows Roux's model, but with branches tending to the phyllomorphic state. Both are Flacourtiaceae. Because of this architecture, *C. bracteifera* has a broad, shallow, monolayered, shade-adapted habit. In all 10 species, tree architecture is very simple (Fig. 2.5). Their photosynthetic organs, mostly large leaves, or small ones arranged in phyllomorphs, form a single subapical layer, minimizing mutual shading within the crown.

The second group contains 13 examples (Table 2.2), and shows greater crown heterogeneity. The only common feature is the plagiotropic orientation of branches or branch complexes (plagiotropy by apposition). This is an expression of shade-tolerance. However, the degree of shade-tolerance varies considerably, ranging from *Himathantus articulatus* (which is found in young secondary thickets near Cayenne) to *Miconia plukenetii* or *Quararibea turbinata*, both of which are found only in mature forest understoreys.

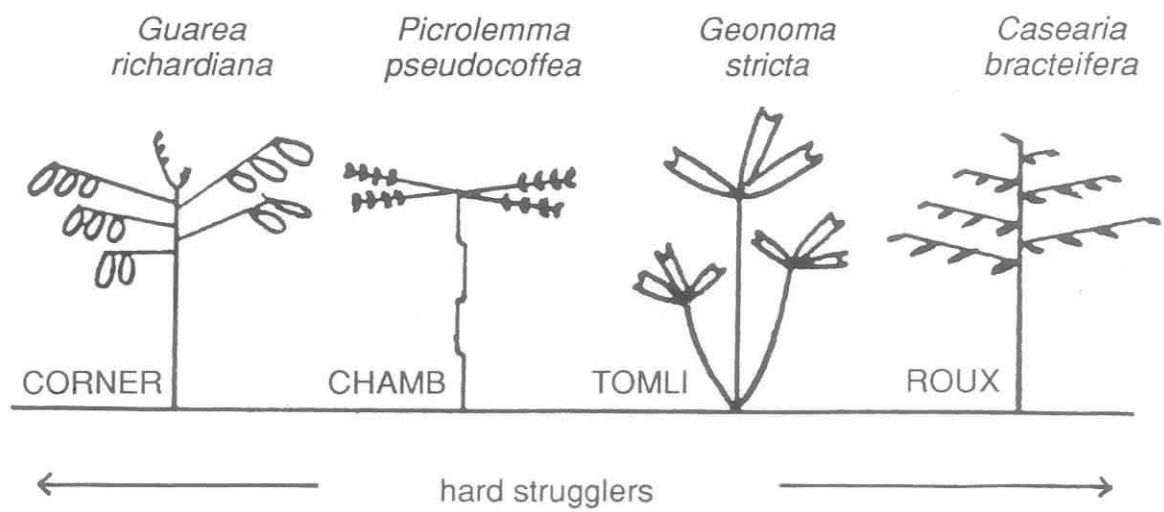


Fig. 2.5 Four examples of hard strugglers from the rain forest in French Guyana, with their typical "simple and poor" architecture and horizontal leaf arrangement; also see Table 2.5. From Oldeman (unpub.)

The species displaying Troll's, Roux's and Petit's models have elongated, diffusely branched crowns with sparsely foliated plagiotropic branches or branch complexes, minimizing mutual shading. *Mouriri francavillana* alternates between Mangenot's model and Massart's model (Oldeman 1974*a*) and so displays great flexibility in leaf arrangement by either spacing the branches apart (Massart), or placing them closely over each other (Mangenot) in an elongate crown, indicating that this species may grow to a considerable height. Distinct superposed branch tiers, plagiotropic by apposition, are found in *Byrsonima* cf. *verbascifolia* (not the savanna genotype) and *Quararibea turbinata*, both conforming to Fagerlind's model. Mutual shading by branches may be great. *Himatanthus articulatus* may also have such a pagoda-like crown architecture, but in more open habitats the modules of branches displaying plagiotropy by apposition form orthotropic shoots. This is an indication of the flexibility of Koriba's model, shown by *H. articulatus*. *Miconia plukenetii* has the same model, but its subapical, rather large leaf clusters on orthotropic axes are true monolayers, like those in the first group.

Strugglers, gambling strugglers and struggling gamblers

Twelve examples of strugglers, gambling strugglers and struggling gamblers can be distinguished, mostly capable of living in the upper canopy (Table 2.3). Their adult stages are light-demanding, but the juveniles show different light requirements. Architecturally, monopodial height growth and intermittent branching are common features.

In Massart's and Aubréville's models, with their plagiotropic branches or branch complexes, this structure results in pagoda trees (see above). In Rauh's model, with orthotropic branches, the growth habit resembles a candelabrum, with essentially monolayered subapical leaf clusters. Examples like *Aniba* sp., *Tetragastris altissima* and especially *Eriotheca* sp. with its large palmate leaves, quite closely resemble pioneer trees like *Cecropia*, *Musanga* or *Macaranga* species (see earlier). This resemblance indicates that the examples cited have gambler strategies and are among the least shade-demanding species in their juvenile state.

More shade-tolerant examples have plagiotropic branches or branch complexes, with marked differences in foliage density denoting different tolerance ratings. *Pourouma minor* and *Manilkara bidentata* (both Aubréville's model) show a very dense and even foliage on plagiotropic branch complexes. *P. minor*, a tree 5 m in height, may have as many as four superposed branch tiers. Monopodial branches in Massart's model have a lower leaf density and therefore less mutual shading of superposed tiers. The number of branch tiers, number of branches per tier, and degree of branch ramification all co-determine the leaf arrangement and density within one crown, linked to tolerance. *Iryanthera hostmannii*, with five branches per plagiotropic tier of Massart's model, is probably less shade-tolerant than *Aspidosperma* sp. with three.

In short, the examples considered range from the struggler to the struggling gambler temperaments (Fig. 2.6). *Aniba* sp., *Tetragastris altissima* and *Eriotheca* sp. are the least tolerant species, *P. minor* and *Manilkara* sp. are somewhat more tolerant. *Iryanthera* sp. is quite tolerant and *Aspidosperma* sp. is most tolerant, although this is not the case for all species of this genus.

Among the species with sympodial height growth, *Cordia* species (Boraginaceae, Prévost's model) have a marked pagoda habit, although their plagiotropic branch modules bear leaves in lower densities than pagoda trees in Aubréville's model. Therefore, their shade tolerance may be comparable to that of trees conforming to Massart's model, converging leaf arrangements being carried on crowns showing the two kinds of plagiotropy. In *Theobroma speciosum* (Nozeran's model), the plagiotropic branch tiers are confined to the upper parts of the sympodial trunk, giving the tree a monolayered crown and shade tolerance. This relative of the cocoa tree indeed lives in deep shade below the forest canopy. *Aparisthmium cordatum* (Koriba's model) has a rather loose, diffusely foliated crown with potentially little mutual shading of leaves and is indeed shade tolerant.

Like the hard strugglers, the examples described here show that different architectural models can lead to convergent crown characteristics. Crown architecture therefore appears once more as one crown characteristic

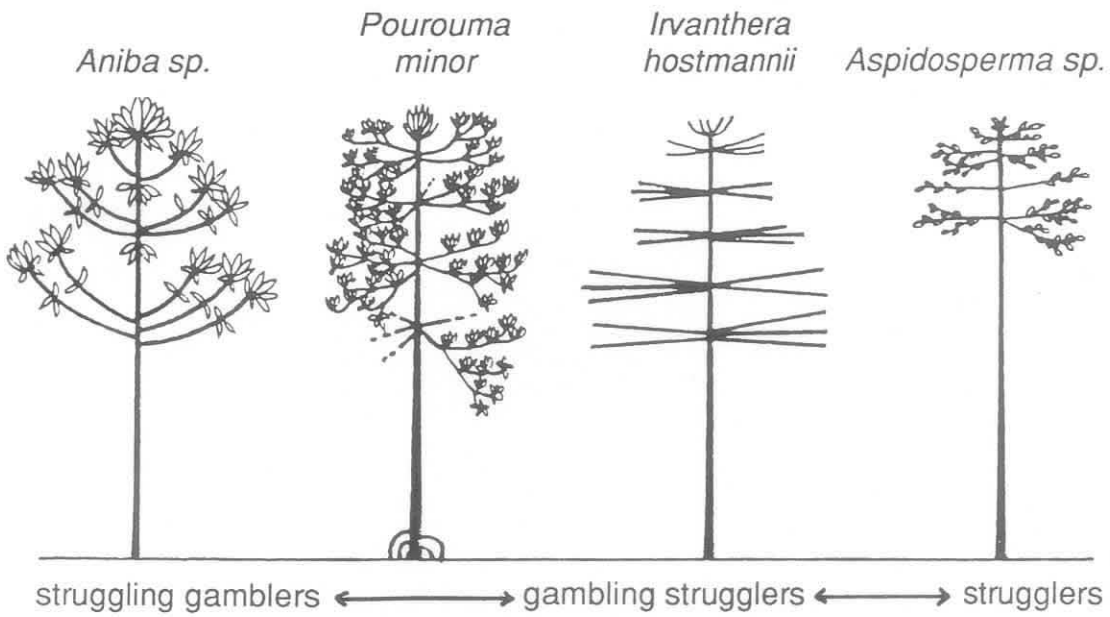


Fig. 2.6 Intermediate temperaments, from strugglers to struggling gamblers. Examples from the rain forest of French Guyana, where they all occur in small to rather small eco-units. Other species of the genera *Aspidosperma* and *Aniba* may behave differently from those observed. Compare with crown characteristics given in Table 2.5. From Oldeman (unpub.)

among others, all being drawn upon in the diagnosis of temperament. Leaf size is also an important feature, Figure 2.6 being consistent with the leaf considerations given earlier.

Gamblers and hard gamblers

Gamblers and hard gamblers are represented by seven examples (Table 2.4), and grow in large eco-units which they colonize. Two groups may again be recognized. The most frequent strategy among these examples is fast height growth at the cost of horizontal crown spreading. *Didymopanax morototoni* (Leeuwenberg's model, Fig. 2.7) has an epicotyledonary axis with prolonged growth up to a height of 10 to 15 m. In this phase, large compound leaves on long petioles are borne in a spiral at the top of the solitary axis (Fig. 2.7A, B). After this monocaul phase, ended by terminal flowering, orthotropic relay axes may prolong height growth by extending vertically. In the mature tree, leaves are very densely packed at the top of terminal modules in a large umbrella (Fig. 2.7C, D). *Jacaranda copaia* follows the same strategy, but its monocaul phase is built sympodially according to Chamberlain's model. *Toulicia guianensis* is similar to *J. copaia*, but data are scarcer.

Height growth concentrated on one orthotropic axis also characterizes the long-lived pioneers mentioned above, namely *Ceiba pentandra* (Massart's model with secondary plagiotropy) and *Goupia glabra* (Roux's

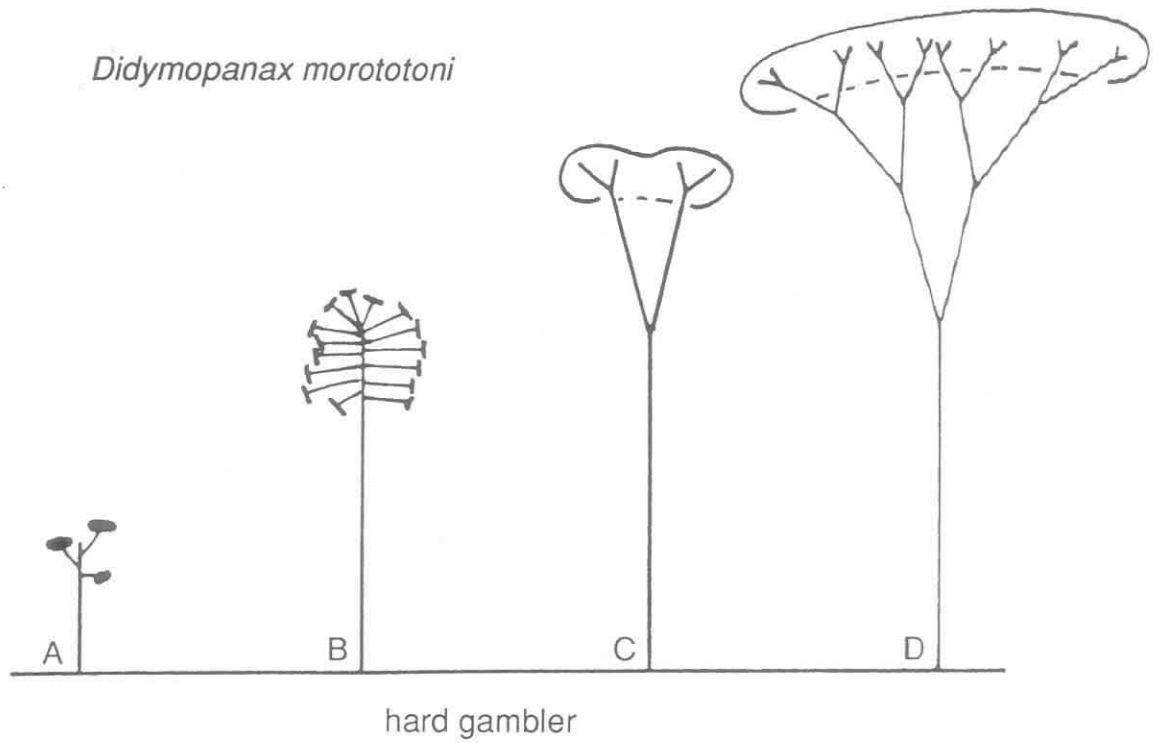


Fig. 2.7 A hard gambler: *Didymopanax morototoni* (Araliaceae) from French Guyana (Oldeman, unpub.). This species occurs in large to very large eco-units ("early succession") and initially show fast, monopodial height growth (A, B) before entering a period of crown spreading, here according to Leeuwenberg's model. For other crown characteristics see Table 2.5

model). They attain heights of over 50 m and persist a long time as emergent survivors of large pioneer eco-units (cf. Hallé *et al.* 1978), while passing their juvenile stage exactly like the common short-lived pioneers. As a matter of fact, juvenile *Goupia glabra* trees in a large, young eco-unit show a striking and profound likeness with the short-lived pioneer tree *Trema occidentalis*, with which it is often confused. Their strong monopodial growth is coupled to rhythmic (*C. pentandra*) or continuous branching (*G. glabra*). The juveniles of these trees are rather sparsely branched, but gradually the trees shift towards more elongate and more densely foliated crowns showing a tendency to multilayering.

The second group of examples follows a completely different strategy (Troll's model, Fig. 2.8). *Annona paludosa*, a pioneer from the tree savannas around Cayenne, and *Apeiba burchellii*, a rain forest pioneer, build densely foliated, spreading, phyllomorphic crowns. They already outshade competitors when juvenile, by occupying the crown space horizontally (Fig. 2.8A). Height growth is accomplished in these species by secondary erection of the basal part of the central plagiotropic axis (Fig. 2.8B, C), and, in other species, by sympodial addition of phyllomorphs of the same kind. This last growth pattern is found in many Leguminosae (see above) and is very flexible.

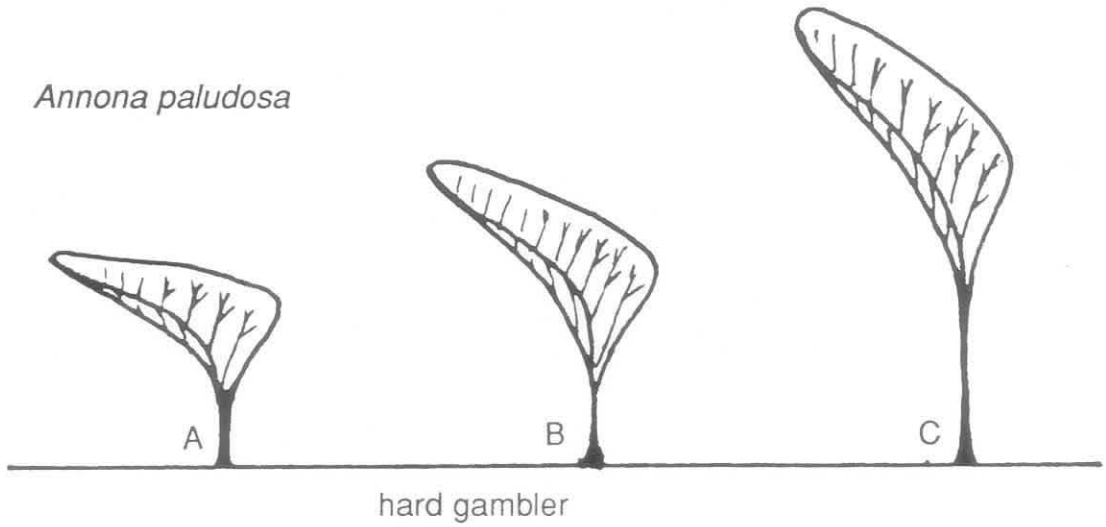


Fig. 2.8 A hard gambler: *Annona paludosa* (Annonaceae) from French Guyana (Oldeman, unpub.). This species occurs in eco-units on poor soils where the forest regenerates very slowly. Other hard gamblers following this architectural principle of phyllomorphic crowns occur in less extreme, large forest eco-units and produce sympodial sequences of such phyllomorphic elements (e.g. *Apeiba burchelli*). Also see Table 2.5

DISCUSSION

On the basis of the preceding data and interpretations, a tree temperament classification that is testable in the field can be tentatively established (Table 2.5). Various crown forms, leaf arrangements and architectural features are classified in the table according to their hypothetical ecological functions, in terms of species strategy, successional status, origin of eco-unit (kind of gap), light requirements and shade tolerance.

Columns A to D (Table 2.5) show hard gamblers and gamblers, and their leaf arrangements. These range from monocaulous or sparsely branched, monolayered trees like *Cecropia* species and others (see above) in column A, to the elongate, multilayered crowns of long-lived pioneers like *Ceiba pentandra* and others in column D. In between, leaves are densely packed – as in fan palms (column Ba) or *Didymopanax*-like umbrellas (column Bb) where mutual leaf shading is enhanced – or by contrast are spread in overtopping phyllomorphs outshading competitors (column C).

Columns E and F mainly concern the intermediate temperaments of struggling gamblers and gambling strugglers. Feather palms (column D) are abundant in small eco-units, frequently appearing in forest mosaics with high dynamics. Other specialists of these environments are pagoda trees or paucilayers, shown in column F as other "small-gap specialists". The density of the foliage within each crown will determine shade tolerance, according to the criteria enumerated above, i.e. number of branch tiers, distance between them, organization of each branch or branch complex and

its foliation. The higher the density, the more mutual shading there is amongst leaves, and more light is required.

Column G shows strugglers with elongate but diffusely branched crowns. Again, their degree of tolerance is determined by foliage density according to the criteria mentioned. Column H contains simply constructed, monolayered hard strugglers completing their life cycles in the shade of the undergrowth near the forest floor.

Table 2.6 is a condensation of the preceding tables, and recapitulates the most important diagnostic characters for establishing tree temperaments by visual criteria. Observation of these criteria, which are physiognomical, architectural and morphological, may serve to establish a diagnosis of the status of a forested surface. The preponderance of hard gamblers and gamblers, for instance, indicates large-scale deforestation in the past, having created large young eco-units. On the other hand, the presence of many strugglers points to a forest having been subject to small-scale disturbances of low intensity (e.g. Pickett and White 1985), and such a forest mainly contains small, mature eco-units. In an inverse way, knowledge of tree temperaments is useful in the design of silvicultural systems for certain management aims.

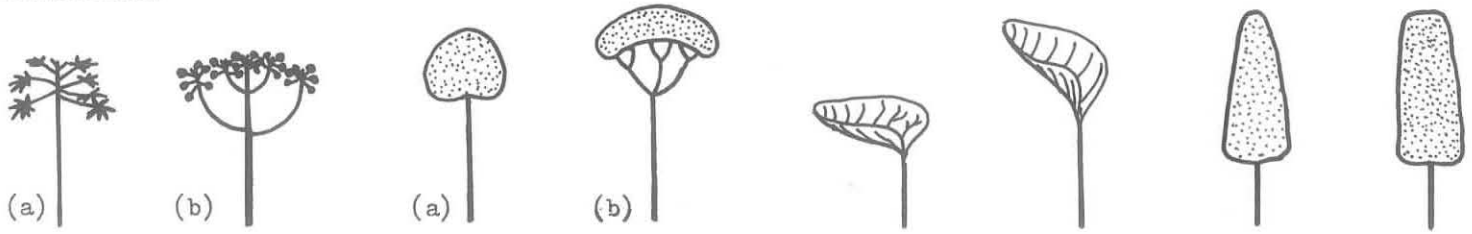
If the diagnosis of tree temperament can be made in a juvenile stage, as has been advocated here, it may contribute to the ecological diagnosis of the eco-unit composition of a forest mosaic ("forest diagnosis"). It may also provide silvicultural insights for forest managers, in facilitating their intervention early in the development of managed stands, before developments have begun that conflict with the management aims.

THEORY AND PRACTICE: RECOMMENDATIONS FOR FURTHER RESEARCH

As shown above, in many silvicultural and ecological concepts and theories, two contrasting temperaments are described, sometimes with intermediates (Mayer 1980). For the tropics, we may list the following pairs although the list is certainly not exhaustive.

- heliophiles (light-demanding) versus sciadophiles (shade-bearers);
- pioneers versus primary species (cf. Whitmore this volume), which is
- analogous to nomads versus dryads (van Steenis 1958) or scar species versus forest species (Mangenot 1958);
- multilayers versus monolayers (Horn 1971);
- r-strategies versus K-strategies (e.g. see Hallé *et al.* 1978, for trees);
- weed trees versus long-lived trees (Corner 1952);
- gamblers versus strugglers (Bazzaz and Pickett 1980).

Table 2.5 Tree temperament classification

CROWN PHYSIOGNOMY (schematic)	 A B C D			
Temperament	hard gambler	hard gambler	hard gambler	gambler
Leaf arrangement	mnolayer	spherical to hemispherical	phyllomorphic (s.l.)	multilayer
Successional status	early successional	early successional	early successional	later successional
Origin of eco-unit	large gap	large gap	large gap	medium-sized gap
Light requirement and shade tolerance	light-demanding shade-intolerant	light-demanding shade-intolerant	light-demanding shade-intolerant	light-demanding some tolerance
Common architectural models	Corner, Holttum (a) Rauh, Scarrone (b)	Corner (a) Leeuwenberg (b)	Troll	Rauh, Massart Roux, Attims
Branch architecture	(a) unbranched orthotropic leader, most often monopodial, few large leaves at the apex; (b) orthotropic leader with few orthotropic branches and large leaves	(a) single, unbranched orthotropic leader with large palmate leaves; (b) tridimensional sympodium with large, compound leaves densely packed on outer shoot ends	main axis mixed; proximal part erect, distal part horizontal with many densely foliated and strongly ramified branches; height growth by further erection of main axis	single orthotropic leader with ortho-tropic or plagio-tropic branches or branch complexes
Examples	(a) first life stage of many pioneers, e.g. *Cecropia*, *Jacaranda*, *Didymopanax*; (b) *Musanga*, *Cecropia*, *Macaranga gigantea*	(a) 'fan palms'; (b) *Didymopanax morototoni*, *Jacaranda copaia*, *Toulicia guianensis*	*Annona paludosa*, *Apeiba burchellii* (latter sympodial)	Gymnosperms; *Trema*, *Macaranga hypoleuca*, *Goupia glabra*, *Ceiba pentandra*

(continued)

Table 2.5 continued

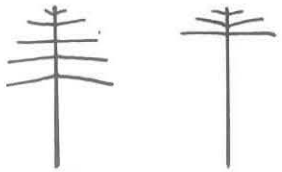
CROWN PHYSIOGNOMY (schematic)	E	 F	G	H
Temperament	Struggling gamblers, gambling strugglers	struggling gamblers, gambling strugglers, strugglers	strugglers, hard strugglers	hard strugglers
Leaf arrangement	'umbrella'	'pagoda', paucilayer	elongate, 'diffuse'	monolayer
Successional status	later successional	later to late successional	late successional	late successional
Origin of eco-unit	intermediate/small gap	small gap	small gap or no gap	no gap
Light requirement and shade tolerance	shade-tolerant to intolerant favoured by light	shade tolerant to intolerant favoured by light	shade tolerant, favoured by moderate light levels	very shade tolerant, favoured by moderate light-levels
Common architectural models	Corner, Tomlinson	Aubréville, Massart	Troll, Roux and others	Chamberlain, Corner, Roux, Cook
Branch architecture	single, unbranched orthotropic leader with large pinnate compound leaves	single orthotropic leader with distinct tiers of plagiotropic branch complexes; shade tolerance determined by number of tiers, distance between tiers and density of foliation within one tier	great architectural flexibility, but crowns with diffuse branching , plagiotropic branches and sparse foliation	'poor' and simple crown architecture, size very small, short orthotropic leader with either few large leaves at the top, or few sparsely foliated (phyllomorphic) branches near the top
Examples	'feather palms'	species of *Terminalia*, *Manilkara*, *Pourouma*, *Iryanthera*, *Aspidosperma*	species of *Anaxagorea*, *Duguetia*, *Hirtella*, *Perebea*	species of *Pavonia*, *Guarea*, *Casearia*

Table 2.6 The important diagnostic characters for establishing tree temperaments

Temperament	*hard struggler*	*(hard) strugglers*	*gambling strugglers struggling gamblers*	*gamblers, hard gamblers*
Orientation	horizontal	horizontal to vertical	vertical	vertical, sometimes sympodia of horizontal elements
Branch distribution	unbranched or subapical	diffuse or subapical	distinct tiers	see Table 2.5
Common architectural models	Chamberlain, Corner, Roux	Troll, Roux	Aubréville, Massart	Rauh, Troll, Leeuwenberg (but see Table 2.5)
Height growth	monopodial or sympodial	sympodial or monopodial	mostly monopodial	monopodial or sympodial
Branch orientation	plagiotropic	plagiotropic	platiotropic or orthotropic	orthotropic or plagiotropic
Branching	diffuse, if any	diffuse	mostly intermittent (rhythmic)	diffuse or intermittent (rhythmic)
Higher-order branching	sparse	sparse	abundant	sparse to abundant (age)
Leaf arrangement	very little leaf surface in single apical layer	little leaf surface sparsely distributed through the crown	leaves more or less densely packed in several distinct layers	see Table 2.5
Leaf size	large if unbranched, small if branched	small	small	often large

Shugart (1984) required more refined temperaments for his Kiambram model in species-rich Australian forests, and therefore resorted to a matrix of four, the pairs being trees that cause or do not cause large gaps when falling and trees that require or do not require large gaps to germinate. He gave no criteria for the diagnosis of these temperaments.

Dualistic classifications are only elegant in appearance. On the one hand, they neglect site factors other than light (e.g. soil, water and biotic factors). On the other hand, they neglect the dynamics of all factors, including light, which cause many tree species to have to face several successive crown environments in growing up. However, it has to be agreed that light availability modulates the intrinsic photosynthetic performance, and so influences all metabolic processes in a tree. Hence light is indeed an essential factor, which justifiably is considered first and foremost. This is what has been done in Tables 2.5 and 2.6, in which all criteria refer directly or indirectly to photosynthesis, including reproduction.

Because adaptation to actual conditions and adjustment to changing conditions are often conflicting, many trees do one after the other instead of reaching a compromise. If changes in their environment are predictable, which in fact they are as far as they depend on eco-unit development (Fig. 2.1), flexible temperaments (Fig. 2.4) can also be predicted. This is most apparent in juveniles, because mature trees, in mature eco-units, face environmental change of a macroclimatic and therefore more stochastic than structural nature (e.g. Vooren and Offermans 1985).

In tropical rain forest mosaics, the diversity in size and architecture of eco-units is much greater than in temperate forests. This explains both the incompleteness of temperate-based theories like that of Horn (1971) in the tropics, and a higher flexibility in the temperament of many tree species than was previously recognized. For instance, species like *Musanga cecropioides* (Florence 1981, in Gabon) or *Cecropia* sp. pl. (Holthuijzen and Boerboom 1982, Suriname) were considered as completely light-demanding, until it was proven that they can germinate in conditions of between 40% and 100% of full sunlight. Using the criteria of Table 2.5, they can therefore be placed more precisely between the extremes of hard gamblers (pioneers) and hard strugglers (very shade-bearing species), on condition that enough information on their behaviour is available. This information should cover the whole life cycle of a tree species, in view of late adjustments in temperament (Fig. 2.4).

The intrinsic leaf properties remain a determinant of tree temperament which is difficult to assess visually. However, this does not render worthless the other criteria. It introduces a vagueness in classifications like the one in Table 2.5, which could be corrected by taking into account the silvicultural growth rates of the species examined, given that cambial activity is a parameter for the whole metabolic performance of a tree which is

determined in the first place by photosynthesis (cf. Oldeman 1974*a*, 1978).

The growth rates of trees are most often a central criterion in silviculture, because forest management most often aims at wood production. Innovative operational systems of high quality, implemented by motivated people, are too often neglected as decisive factors in strategic planning of enterprises, as has been proven by a McKinsey and Cy team (Peters and Waterman 1982). It is our claim that one of the key factors for improving the silvicultural quality of forest management enterprises in the tropics is the knowledge of tree temperaments, because this is essential in promoting the growth of the trees to be harvested. The same is true in the case of other management aims requiring the growth of healthy trees, e.g. in protection forestry and nature conservation management.

Choosing tree species with the wrong temperament to implement a silvicultural system is an error in both ecological and economic terms. Keeping trees alive and growing in an environment to which they are not optimally adapted costs work and money, in the form of many silvicultural interventions. Generally, such increased cost is not warranted by increased income. This is an empirical truth, supported by the history of forest management.

Figure 2.9 illustrates the role of tree temperaments in different regeneration systems. Selective cutting (only a few trees being harvested per hectare), is contrasted to all-timber cutting (e.g. if all sizes over 25 cm diameter in all or most tree species are cut for pulp production). Selective cutting favours forest regeneration involving many strugglers and gambling strugglers (Table 2.5). All-timber cutting, leaving behind huge young eco-units, will favour hard gamblers, gamblers and to a lesser degree, struggling gamblers. In time, after tens of years, more struggling temperaments will become more frequent in the latter case, when the pioneer forests (gamblers) fall apart.

The temperaments present in populations of juvenile trees can be assessed by examining the criteria mentioned above. Lists of the precise temperament for each useful tree species do not exist as yet. These would be needed for the precise design of high performance silvicultural systems. Preliminary assessment of the temperaments among the juvenile trees at least is a method to estimate the growth potential of groups of wanted species present, even if they may hold surprises in later life (Fig. 2.4).

The smaller the young eco-unit (Fig. 2.1), the higher the proportion of strugglers among the juveniles; the larger the young eco-unit, the more frequent are hard gamblers and gamblers (cf. Fig. 2.9). This simple principle may serve to establish a list of silvicultural systems and required tree temperaments as shown in Table 2.7.

Later silvicultural operations, like tending and liberation thinning, may create the conditions needed to favour certain temperaments among the

Table 2.7 Tree temperaments best suited to silvicultural systems employing different sized regeneration units (eco-units)

Size of regeneration unit (= Eco-unit)	*Temperaments required (Fig 2.4; Table 2.5)*
Large eco-units	
Clear-cutting and plantation	Hard gamblers (strugglers, struggling gamblers may be underplanted)
Clear-cutting and conversion	Hard gamblers, strugglers, and some struggling gamblers for minor products
Clear-cutting and natural regeneration	Naturally prevailing are hard gamblers and gambling strugglers; strugglers and others come in later with succession
Intermediate-sized eco-units	
Strip-cutting and plantation	Depends on exposition and width of strip
Group-cutting and natural regeneration	Strugglers, gambling strugglers, struggling gamblers
Small eco-unit	
Selective cutting and natural regeneration	For recruitment, mainly hard strugglers, strugglers, gambling strugglers and struggling gamblers. For ingrowth of higher trees of the future, mainly strugglers and struggling gamblers

trees present. This implies a shift in the natural spectrum of temperaments, which should be compatible with both the vulnerability to abrupt increase of light in trees with more struggler-like temperaments (see above) and the further development of vital eco-units (cf. Figs. 2.1 and 2.9).

These silvicultural techniques can be applied in order to reach different management aims. One example of the correct use of tree species with different temperaments is illustrated in Figure 2.10. Figure 2.10*a* shows large-scale plantations of *Acacia mangium* (foreground, left) and *Eucalyptus* species in East Kalimantan (Indonesia) on sites that had been cleared by forest fires in 1982 and 1983. These trees are hard gamblers, with high wood production rates. The risks implied in creating such huge, homogeneous eco-units are determined by "hidden" heterogeneity, left over from the past history of the site, like surviving sources of pathogens and parasites or soil differences, and by genetic heterogeneity in the planted tree populations. Indeed, this leads to local tree mortality. Wherever this occurs, a smaller young eco-unit is formed (Fig. 2.1). Here, conditions would be propitious for species with other temperaments, such as Dipterocarpaceae (Fig. 2.10*b*).

Human-induced processes at Forest Mosaic level				
	A. SELECTIVE CUTTING (★= to be cut)		B. ALL TIMBER ●	
Cutting (= to be cut)				
Consequences		*		*
1. ARCHITECTURE	– changed eco-unit distribution	+	– some large eco-units	–
	– lateral gradients eco-units	++	– lateral gradients eco-units	±
	– form eco-units	+	– form eco-units	–
	– changed micro/mesoclimate	+	– change micro/macroclimate	–
2. ENERGY, NUTRIENTS, WATER	– soil compaction, permeability (localized)	±	– soil compaction permeability (all-over)	–
	– erosion	+	– erosion	–
	– leaching (localized)	+	– leaching (generalized)	–
	– energy and matter flows	+	– energy and matter flows	–
3. COMPONENT SPECIES	– richness flora and fauna	++	– richness flora and fauna	±
	– diversity changes	++	– diversity changes	–
	– participants in diversity (species)	+	– participants in diversity (species)	–
	– soil flora and fauna	+	– soil flora and fauna	–

Please note that diagnosis will be different according to site (LMU) and technology applied

* Reversibility of effects ++ very fast + rather fast ± within 1 tree-lifespan – longer than 1 tree-lifespan

Fig 2.9 Selection of tree temperaments in tropical rain forest under two wood harvesting regimes, i.e. selective cutting of two to five marketable timber trees per hectare (A) and cutting of all pulpable wood of most species over a diameter limit, e.g. 25 cm dbh (B). In the first case, rather small gaps give rise to small eco-units, favouring the germination and establishment of trees towards the struggler side of the spectrum of temperaments (Table 2.5). In the second case, large clearings are created, on which large eco-units are built by trees having temperaments towards the gambler side of the spectrum depicted in Table 2.5. Criteria for establishing a **forest diagnosis** before and after such interventions are discussed by Oldeman (1987), which is the source of this figure. The diagnosis given here is a rough approximation because present knowledge does not allow greater precision. "Tree life span", for instance, would average some 50 to 70 years. LMU = Land Management Unit, a concept from land evaluation

Fig. 2.10 Above – Extended plantation of *Acacia mangium* (foreground left) and *Eucalyptus* species on sites homogenized artificially after large-scale forest fires in East Kalimantan (Indonesia) in 1982 and 1983. Note standing burnt trees. The crown canopy pattern in the plantations, less than a year old, shows patches of different tree vitality among the hard gamblers planted here. Such patches become small gaps if these trees die, and give rise to small eco-units in which other temperaments would be favoured, (e.g., the struggling gamblers among the Dipterocarpaceae, if seedlings were present). Below – Such seedlings are underplanted by the Indonesian forest enterprises since the development of appropriate nursery techniques. These struggling gamblers are Dipterocarps and the juveniles display Massart's or Roux's model (shown here). They provide for sustainable wood production either after harvest of pioneers or their untimely death. Photographs Oldeman (1986)

Indeed, underplanting with struggling gamblers such as *Shorea* species (Dipterocarpaceae), grown and inoculated with the right mycorrhizae in nurseries (Smits *et al.* 1987), is now advocated as standard practice in the management of these forests (Soeryono 1987).

Knowledge of tree temperaments is thus considered indispensable in the design of silvicultural systems, because there are no standard recipes for such systems. The above example shows how problems have been addressed in one situation, but each site in each forest region – with its particular floristic composition – demands silvicultural systems which are tailor-made for that situation. The same is true for agro-forestry systems and their tree species.

However, those responsible for designing silvicultural systems in the humid tropics face the difficult problem of transforming a highly heterogeneous forest (cf. Mutoji-A-Kazadi 1977) into a forest that can be managed. Monocrop plantations tend to become more heterogeneous, as illustrated above. Moreover, they are problematic from the viewpoint of sustainability (Jordan, this volume). And polycyclic, multispecies systems (e.g. de Graaf 1986, Jonkers 1987) require the introduction of sufficient homogeneity to make them manageable, and like plantations have to be sustainable as to energy, water and nutrient cycling (e.g. Poels 1987).

Some rules-of-thumb can be put forward in this context.

- The diagnosis of the forest has to be made in terms of trees to be cut and trees to be left over, so as to keep the matrix of the forest (we would say: its eco-unit composition) sustainable and manageable.

- This diagnosis should concern not only marketable trees, but also other species and decaying trees, with the aim of conserving habitats for future wanted trees.

- After harvest according to such a preceding diagnosis, a selection should be made among the juvenile trees left behind, including all species that may conceivably become marketable in the future, and those juveniles should be favoured by silvicultural measures appropriate to their temperament.

- Considerable reduction of the number of species is possible, but is often difficult to handle.

- Forest treatments always, and automatically, select tree species according to their temperaments. With a wrong diagnosis, treatments will favour unwanted trees.

These "rules" can be easily modified in order to fit in with management objectives other than that of wood production. As a matter of fact, such rules tend to optimize the harmonization of trees with a certain temperament and their forest environment. We have seen, in the above paragraphs, that this question is more complicated than it seems at first sight, particularly in the humid tropics. Temperaments are determined by the tree's organs, its organ-bearing shoots, and its overall architecture, and by the interactions between these levels of organization. The immediate environment of a tree, the eco-unit which it inhabits, is determined by the surrounding forest and by abiotic factors, as well as by the interactions between these levels.

The concept of tree temperament is, therefore, crucial in forest management, and the following recommendations are proposed for promoting its further study.

(1) Support or establishment of study groups on life cycles and temperaments of forest trees belonging to the main families in the rain forests of different continents, e.g. *Leguminosae*, *Dipterocarpaceae*, *Lauraceae*, *Vochysiaceae*, *Meliaceae*, *Chrysobalanaceae* and others.

(2) Support or establishment of study groups on life cycles and temperaments of particular forest tree species, determining the rain forest matrix over long time spans, and selected by ecological and economic criteria.

(3) Stimulation of studies on neglected life phases of such trees, particularly the juvenile phase.

(4) Inclusion in tree temperament studies of associated organisms, e.g., mycorrhizal fungi, other microflora and microfauna (Jordan, this volume), epiphytes, lianes, herbs, larger animals.

(5) Inclusion of tree temperament studies in many other rain forest projects, by asking the researchers to unite data files on certain tree species in a standardized and low-cost way, so that a rich data stream may contribute to the building-up of central files.

(6) Creation of a tree temperament periodical, as a forum for publishing new studies and updating the knowledge on many tree species in a regular way, in a form comprehensible to forest managers.

(7) Accumulation of experimental data on tree temperaments (cf. Bongers and Pompa 1988), by growing tropical rain forest patches

(eco-units) *in vivo* or *in vitro*, under controlled conditions and circumstances.

(8) Preparation and formulation of simulation models for the growth of trees with different temperaments, the outputs of which should be both numerical and graphical.

(9) Identification and collation of urgent questions to be answered by researchers, by screening many forest management plans in the humid tropics, with the help of the managers.

(10) Raising of awareness among tropical forest ecologists and silviculturists that tree temperaments are both essential to the understanding of rain forest dynamics and much more complex than is suggested by previously published simple classifications.

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